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CONTENTS

ERRATA

Page 76, line 9, *for* lenger *read* longor.

119, line 2 from bottom, for *Pimelia* read *Pimelea.*

121, line 18, for *Pimelia* read *Pimelea.*

121, line 18, for *prostata* read *prostrata.*

126, line 5, for *Dianthonia* read *Danthonia.*

128, centre, for *Pimelia* read *Pimelea.*

186, line 7 from bottom, for *Jepsoni* read *Jepsonii.*

208, line 10 from bottom, for *Pimelia* read *Pimelea.*

221, line 25, for *Diatomah* read *Diatoma.*

226, line 22, for *Paralia sulcata* read *Melosira (Paralia) sulcata.*

231, line 6 from bottom, for *faeroensis* read *faerocensis.*

231, line 6 from bottom, for *Stephanopyxis* read *Stephanoplyxis.*

234, line 19, *for* × 1,000 *read* × 660.

234, line 12 from bottom. *for* × 2,000 *read* × 1,320.

234, line 4 from bottom, for var. *producta* read var. *intermedia.*

236, line 20, *for* × 1,000 *read* × 660.

249, line 25, for *N. Legumen* read *S. Legumen.*

252, line 15, for var. *producta* read var. *intermedia.* Add to the description :—
L. 45–65 μ, b. 11–15 μ.

263, line 6, for *latistriatae* read *latistriata.*

266, line 11 from bottom, for *attentuatum* read *attenuatum.*

304, line 1, for *laciniosus* read *laciniosum.*

305, line 3 from bottom, for var. *producta* read var. *intermedia.* Add to the description :—45–65 μ longis, 11–15 μ largis.

307, centre, for *amphioxis* read *amphioxys.*

434, line 24, *for* Link. *read* Link

508, centre, for *Engleriana* read *Englerianum.*

568, line 7 from bottom, *for* 1064 *read* 564.

568, line 4 from bottom, *for* 1065 *read* 565.

569, line 9, *for* 1309 *read* 809.

569, line 9, *for* 1310 *read* 810.

569, line 9, *for* 1348 *read* 848.

577, centre, *for* 1064 *read* 564.

585, line 7, *for* 1065 *read* 565.

589, line 17, *for* 1310 *read* 810.

648, line 2 from bottom, for *appennina* read *apennina.*

EXPLANATION OF THE PLATES

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On a *Scolecopteris* (*S. Oliveri*, sp. n.) from the Permo-Carboniferous of Autun.—
I. The Fructification. By D. H. SCOTT, M.A., Ph D., F.R S., F.L.S.

(PLATES 1 & 2, and 2 Text-figures)

[Read 23 October 1930]

IN 1901 my friend Professor F. W. Oliver, F.R.S., visited Autun, and brought
back a number of specimens of the petrified plant-material from the Permo-
Carboniferous of that locality, so famous for the researches of Bernard Renault.
We agreed to divide the material between us. A certain number of sections
were cut at once ; other blocks were put aside, and have only recently been
sectioned. The new sections were cut for me by Mr. W. Hemingway. Among
them was a slide which he described as ' Filicoid leaves and sporangia. ? *Scole-
copteris* or *Asterotheca*.' It is a remarkably good section, crowded with leaflets,
some of which bear sporangia. For reasons to be fully stated below, I deter-
mined the genus as *Scolecopteris*, one of Mr. Hemingway's alternatives. A few
days later he sent me eight more sections from the same block, all of which
show more or less of the sporangia. There are thus nine sections in all. They
appear to form two unequal series. Two sections (148.1 and 148.2) are
clearly adjacent, and the remaining seven form a continuous series, which I
was able to arrange in order.† They are numbered 148.2* to 148.8. I have
not been able to correlate the two series exactly, but all the nine sections were
evidently cut very near together.

† In this and other points I was materially assisted by my late wife, Mrs. D. H. Scott, F.L.S.

All the sections are closely packed with pinnules, lying in irregular layers. Most of them are sterile, but some bear the synangia, which are remarkably well shown (see the Plates). Not all the sterile leaflets, as shown in section, are alike. While we have sufficient evidence that the majority belonged to the same species as the fertile pinnules, others are probably of a different nature. A few other extraneous fragments also appear to be present. Here and there a rachis is seen in section, probably forming part of the *Scolecopteris* frond.

In the present paper the fertile pinnules and their synangia will be described, as on their characters the determination of the genus depends. The structure of the vegetative organs (sterile pinnules and rachis) will be dealt with in a subsequent paper by Professor H. S. Holden and myself.

The Synangia.

Although the habit of our species is not known, there can be no doubt, from the analogy of all the allied Permo-Carboniferous Ferns (of the form-genus *Pecopteris*), that the frond was a large and highly compound one—at least tri-pinnate.

The sections showing the fructification are for the most part cut across a series of fertile pinnules, evidently belonging to the same secondary pinna of the frond (Pl. 1. figs. 1 & 2). The sections, however, are oblique, as shown by the fact that a rachis, presumably that of the pinna, is present, in oblique transverse section, interrupting the series of fertile pinnules (Pl. 1. fig. 1). Nevertheless, the action of a pinnule is sometimes sufficiently transverse to show clearly the position of the synangia (Pl. 1. fig. 3). In the case cited there are two synangia shown, one on each side of the midrib. The margins of the pinnule are strongly incurved, so as almost to overlap the synangia (best seen on the right, in Pl. 1. fig. 3). Evidently the arrangement was just the same as in the well-known case of *Scolecopteris elegans* (Strasburger, 1874). There was thus a longitudinal row of synangia on either side of the midrib of the pinnule, as was usual in fossil plants of this affinity.

That the synangia were borne on the lower side of the pinnule is obvious from the general form of the transverse section, with its prominent midrib. The fertile leaflets are, as a rule, badly preserved, but in a few cases the structure can be made out sufficiently. The palisade-tissue lies near the lower surface, a wide band of aqueous tissue or hypoderma intervening between the palisade and the upper epidermis. This peculiarity is shared by the sterile pinnules which we refer to the same plant (Pl. 1. fig. 4).

In a vertical section of a synangium one usually sees two sporangia only (Pl. 1. figs. 3, 4, 5). There are also sections in a plane parallel to the surface of the pinnule, showing the synangia in approximately transverse or horizontal section. In the case represented in Pl. 1. fig. 6 and text-fig. 1 two of the synangia show plainly four sporangia in each. One synangium, however, shows three only,† and it is possible, though not certain, that no more were present in this

† See Addendum, p. 11,

instance.† Altogether, in various slides, at least eight cases of quadrilocular synangia have been observed. In one case, however, as shown in Pl. 1. fig. 7, a fifth sporangium is clearly present. Here the sporangia are not all cut at the same level, the section being oblique ; there is, however, no doubt that the total number was five. In respect of the number of sporangia, then, our species agrees with those (*S. elegans* and *S. minor*) described by previous observers.

We will now consider the structure of the syngangium more in detail. The constituent sporangia are evidently seated upon a definite pedicel (Pl. 1. fig. 5 ; Pl. 2. figs. 8 & 9). The base of each sporangium is inserted obliquely on the top of the pedicel, the surface of attachment sloping down from the centre to the sides.

TEXT-FIG. 1.
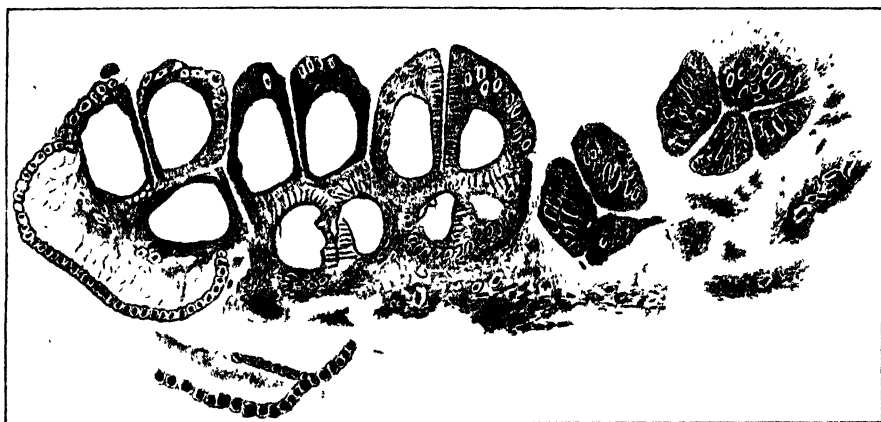
Superficial section of pinnule, showing, in more detail, the group of synangia represented in the photograph, Pl. 1. fig. 6. For description, see text. Parts of other pinnules are also shown. Slide 148.1, × about 30. From a drawing by the late G. T. Gwilliam, F.R.A.S.

The fructification, then, is that of a *Scolecopteris*, as distinguished from *Asterotheca* or *Acitheca*. The last-named genus, originally founded by Schimper, has been revived by Kidston. While in *Scolecopteris* the sporangia are ' attached to the apex of a short pedicel-like receptacle,' in *Acitheca* they are sessile and for the basal third of their length ' united to a central column ' (Kidston, 1925, pp. 535–537). In *Asterotheca* the synangia are sessile on the frond and there is no column or pedicel. It is evident that our plant conforms to the character first given, and is therefore a true *Scolecopteris*.

† In all these synangia the cell-walls are unusually faint, and the appearance suggests that they may have been young. All the cavities are empty, but there is no sign of dehiscence ; possibly the spores, being immature, were not preserved. The degree of cohesion in the quadrilocular sporangia shown is somewhat greater than usual, perhaps only because they are cut near the base. The two synangia towards the right of the text-figure are cut through the apical walls.

The dimensions in the case shown in Pl. **1**. fig. 5 are as follows :—

Total height of synangium .... 1·56 mm.
,,   ,,   pedicel .... ·48 mm.
,,   ,,   sporangium .... 1·32 mm.
Maximum diameter of sporangium .... ·44 mm.
Diameter of pedicel .... about ·40 mm.

The sporangia in other instances attain a somewhat greater height, up to 1·4 mm. The total height of the synangium is considerably less than that of pedicel+sporangium, because the sporangial wall on the outer side overlaps the pedicel for about half its length. It appears that the base of the pedicel was somewhat sunk in the tissue of the pinnule.

The sporangia are of a roughly conical form, with a somewhat pointed apex (Pl. **1**. figs. 3 & 5 ; Pl. **2**. fig. 8). The inner sides, by which they are in contact with one another, are fairly straight, while the external sides are curved. The external wall is two cells or more in thickness at the base, where large short cells occur. Further up, this wall may thin out to a single layer and perhaps it always does so, but a slight obliquity in the plane of section may give an appearance of more layers. The walls on the inner side are one cell thick throughout ; they are thinnest towards the middle (i.e. towards the centre of the synangium) where dehiscence no doubt took place (Pl. **1**. fig. 7).

At the apex of the sporangium the walls become thicker, so that there is a small solid tip, in which some large rounded cells are present (Pl. **2**. fig. 13).

We have spoken throughout of a *synangium,* and the term is no doubt justified, but the amount of cohesion between the constituent sporangia must have been very small. In some of the vertical sections no cohesion at all is shown ; this is presumably in cases where the plane of section fails to reach the middle of the synangium. A fair instance of cohesion is shown in Pl. **2**. fig. 13, where the two sporangia seen are free, except for quite a short distance (two or three cells in length) at the base, a cohesive region scarcely 0·1 mm. in extent. As already pointed out, cohesion is somewhat better shown in some of the synangia represented, in horizontal section, in Pl. **1**. fig. 6 and in text-fig. 1.

In one case (Pl. **1**. fig. 5) there is evidence of a connection between two sporangia by their tips. The tissue appears to be perfectly continuous at this point. I am inclined to think that there was a real apical connection, though I have found no other instance. It would, of course, be easily broken through.

In some of the sections the walls of the sporangia are seen in surface-view (Pl. **1**. fig. 5 ; Pl. **2**. fig. 10). The cells of the inner wall are more delicate and sometimes shorter than those of the outer, though all are elongated, except the roundish cells met with at the base and apex.

Many of the sporangia contain spores (Pl. **1**. fig. 3 ; Pl. **2**. figs. 8 & 9), though others are empty. The spores are small (perhaps somewhat shrivelled) and

measure about 17 or 18 μ in greater diameter. The best-preserved are elliptical in shape. In text-fig. 2 two spores are shown, very highly magnified.[†] The form indicates that they were bilateral and not tetrahedral as described by Strasburger and by Geinitz and Drude (1880) in *Scolecopteris elegans*. The rugose or tuberculate surface, however, agrees with the observations of the latter authors. Though the sporangia are mostly old and had already undergone dehiscence, there is no reason to doubt that the spores which they often contain are their own, and not foreign intrusions.

Practically every sporangium contains a delicate film, densely dotted in surface-view and more or less retracted from the sporangial wall (Pl. **1.** figs. 5 & 7 ; Pl. **2.** figs. 8 & 9). This may well represent the remains of a tapetal layer.

The structure of the pedicel, on which the synangium is borne, is well shown in some of the sections (Pl. **1.** fig. 5; Pl. **2.** figs. 8, 9, & 10). It has a core of somewhat thick-walled short cells, the walls of which have a very clear reticulate sculpturing (Pl. **2.** figs. 11 & 12). In the distal part of the pedicel this core

TEXT-FIG. 2.
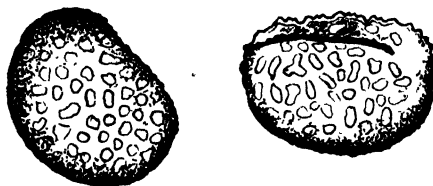
Two spores from a sporangium, showing the elliptical form, rugose surface, and in one case a longitudinal line of junction. Slide 148.4, × about 1500. H. S. H.

is surrounded by an external zone of delicate parenchyma, only occasionally preserved (well shown in Pl. **1.** fig. 5). At the base, where the pedicel is inserted in the tissue of the leaflet, the core of tracheal cells (as they may be called) broadens out, and at the extreme base these elements become narrower and elongated (Pl. **2.** fig. 12). This, no doubt, indicates the connection with a lateral vascular bundle of the pinnule. The narrowest elements appear to show a spiral, rather than a reticulate, sculpturing. In the distal part of the pedicel the cells of the core become thicker-walled and of a dark brown colour, obscuring the details of structure. It appears that the proximal part of this dark region retains the tracheal markings, but that they disappear as the sporangia are approached. The dark brown tissue is, in fact, continuous with the sporangial walls, and approximates to their structure.

In an article in ' Nature ' (March 2, 1929) I shortly referred to *Scolecopteris Oliveri*, and made a statement which I am now convinced was erroneous. I then regarded it as an important feature of the new species that each fertile

† This text-figure was kindly drawn for me by Professor H. S. Holden.

pinnule was immediately subtended by a sterile pinnule. In some of the sections this relation is no doubt conspicuous (Pl. 1. figs. 2 & 4). But I find that is by no means constant, and the suggestion that the pinnule may have been folded on itself is negatived by further observations. The juxtaposition of fertile and sterile leaflets was, I am now convinced, merely accidental.

<center>' •   <i>Comparison with other Species.</i></center>

Only two species of <i>Scolecopteris</i> in the narrower sense here adopted have been described in any detail, <i>S. elegans</i> Zenker and <i>S. minor</i> Hoskins.† Zenker, who founded the genus, gave an excellent description of <i>S. elegans</i> as long ago as 1837.‡ The structure of this Permian species from Saxony is similar in essentials to that of our <i>S. Oliveri</i>. Zenker correctly described the leaflets and fructification, and thought the plant belonged either to the Marattiaceæ or to some extinct group of Ferns. His suggestion of a relation to the contemporary Tree-ferns and to the 'Staarsteine' (<i>Psaronius</i>) is very acute, and probably correct.

Strasburger's work on this species, dating from 1874 and carried out on a thin section (such as was not available to Zenker), has become one of the classics of Palæobotany. We may briefly compare his results with our own.§

Strasburger states that the 'sori' (synangia) are equally often quadrilocular and quinquelocular, though his figures show the former in a majority. The edges of the fertile pinnule are strongly incurved on the lower side, as in ours. The sporangia are united where they are seated on the common pedicel, and diverge above—each ending in a somewhat pointed apex. The sporangial wall is mostly two layers, rarely one layer, in thickness. A third delicate layer is sometimes indicated. The wall is constantly interrupted on the inner side for dehiscence. The pedicel consists of somewhat lax tissue, with a strand of rather narrower cells in the middle. These central cells are described as, for the most part, distinctly porous. The spores found often show the tri-radiate ridge—not all are normally developed.

No measurements are given, but, making use of the magnification of the figures, it appears that the height of the sporangium was hardly 0·9 mm.‖ Total height of the synangium about 1 mm., the pedicel being very short. Spores about 15 μ in diameter. Thus the dimensions are decidedly smaller than in <i>S. Oliveri</i>.

Strasburger's attention was evidently rivetted on the fructification; he gives little detail of the structure of the leaflet on which it was borne. Hence the

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† The well-known species commonly called <i>Scolecopteris polymorpha</i> is now placed in <i>Acitheca</i>. See above, p. 3.

‡ The odd idea, once entertained, that the leaflets were maggots or worms explains the generic name (σκώληξ, a maggot). The history of the specimens of <i>S. elegans</i> was carefully traced by Solms-Laubach in 1883.

§ See Addendum, p. 11.

‖ See Addendum, p. 11.

data for a comparison with *S. Oliveri* are limited. In the general arrangement, and in the structure of the sporangia, we find no definite distinctive characters ; on the other hand, the structure of the pedicel is by no means identical in the two forms—it is less strongly differential in *S. elegans* than in our plant. Strasburger states that the cells of the central strand pass over gradually into the peripheral tissue. In our species there is a sharp limit. Although Strasburger says that the central cells were generally porous, his figures show no distinct pits or markings (Strasburger, figs. 8 & 12). In our case they could not have been missed. In *S. elegans* the central strand is much more slender than in *S. Oliveri* and the form of the cells different (Pl. **1.** fig. 5 ; Pl. **2.** figs. 11 & 12).

The data in Strasburger's memoir thus confirm the impression that the new *Scolecopteris* is distinct from *S. elegans*.

Strasburger's account was supplemented some years later by Geinitz and Drude (1880). They give some good figures, but add little that is new. Drude, in his report on the microscopic structure, states that the spores are sometimes found united in tetrads. His figures indicate that the cohesion between the sporangia was somewhat greater in *S. elegans* than in *S. Oliveri*.

Two other European species were briefly recorded by Grand'Eury (1877) from the Carboniferous of the Loire. In *S. subelegans* his small-scale figure shows the fertile pinnules very little incurved and thus quite different from ours. He also thought an indusium was present.

In his *S. Ripageriensis*, the pinnules are shown incurved, as in ours, but the sporangia are oblong, not pointed, and large, the height of the synangium (according to the magnification) being about 3 mm. It thus appears, so far as the meagre data show, that neither of Grand'Eury's species can be identical with our own.

Dr. Hobart Hoskins has given (in 1926) a full illustrated account of a new *Scolecopteris*, *S. minor*, from the Pennsylvanian coal-balls recently discovered in Illinois, U.S.A. The horizon appears to be somewhat high up in the Coal-Measures. Dr. Hoskins's plant is in many respects much like ours, but the dimensions of the fructification are much smaller. The pinnules are of the *Pecopteris* type, and appear to agree in general form with those of *S. Oliveri*. The sporangia in a sorus (synangium) are usually four or five, the former about twice as numerous as the latter. In one case six were observed. They are only slightly connected at the base, and attached to a common pedicel. The apices of the sporangia are solid and bluntly pointed. The wall usually appears only one cell thick, but two inner layers were sometimes preserved. The outer layer has thick-walled cells.

The height of the sporangium is about 0·7 mm. (about half that in our species) and its diameter 0·28 mm. The spores, however, are about the same size as in *S. Oliveri*, about 17 μ.

The pinnule is described as having one or two layers of thick-walled cells under the upper epidermis. There may sometimes be a slight development of palisade-tissue under the thick-walled layers. Thus the structure, except

for the presence of a hypodermal layer, seems different from that in our species, in which the palisade-tissue is a constant and striking feature. On the other hand, the account of the structure of the ultimate rachis agrees with our observations, which will appear in the subsequent paper.

As regards the pedicel, Dr. Hoskins states that a few spirally thickened elements deploy from the lateral vein and end in the upper portion of the pedicel. There thus appears to be something answering to the tracheal core of the pedicel in *S. Oliveri*, though less developed.

It will be clear from the above summary that *Scolecopteris minor* is a species closely allied to, but distinct from, our *S. Oliveri*.†

Diagnosis.

We may now briefly sum up the main features of the new species, in the form of a diagnosis, to serve for its identification.

SCOLECOPTERIS OLIVERI, sp. n.

Fructification borne on the lower side of the ultimate pinnules of the compound frond, consisting of synangia in two rows, one row on each side of the midrib of the pinnule.

Each synangium consisting of four or occasionally three or five sporangia, ranged in a circle and seated on a definite pedicel.

Sporangia slightly coherent at the base, somewhat pointed at the apices.

Spores ellipsoidal, rugose.

Pedicel with a massive core of reticulately sculptured cells, connected below with a lateral vein of the pinnule.

Fertile pinnule with incurved margins. Palisade-layer deeply seated, separated from the upper epidermis by a broad layer of hypoderma.

Dimensions :—

Width of fertile pinnule	about 2·7 mm.
Total height of synangium with pedicel	1·6 mm.
Height of sporangium	1·32–1·4 mm.
Maximum diameter.....................	0·44 mm.
Spores	about 18 μ

The species is named in honour of Prof. F. W. Oliver, F.R.S., to whom I am indebted for the material.

Affinities.

We have referred our species to *Scolecopteris*, as explained above, on the ground that the synangium is seated on a definite pedicel. As we have only structural material to deal with, and consequently have no direct knowledge of the general habit, this nomenclature seems justified. Max Hirmer, however, while he recognises *Acitheca* as a distinct genus, merges *Scolecopteris* in

† It is a pity that some of the photographs illustrating Dr. Hoskins's paper are less clear than might be wished.

Asterotheca, and identifies the well-known species *S. elegans* with *Asterotheca arborescens* Schlotheim (Hirmer, 1927, pp. 576, 585). Geinitz had already pointed out the close resemblance to that species (Geinitz and Drude, 1880, p. 1).

Certainly *Asterotheca* and *Scolecopteris* are so closely allied that it must often be impossible to distinguish between them, and the latter genus can only be based on material with structure preserved. Such specimens are notoriously difficult to identify definitely with those preserved in the form of impressions.

To come to broader questions of affinity, most writers on *Scolecopteris* and its allies have recognised a relation to the Marattiaceæ, and have assumed that the fossil group belonged to the true Ferns. Zenker, as we have seen, referred *Scolecopteris* either to the Marattiaceæ or to some peculiar tribe of Ferns and suggested a relation to the contemporary Tree-ferns and *Psaronius*. Strasburger discussed the affinities of *Scolecopteris* very fully ; he had no doubt that the plant, as shown by its sorus-formation, belonged to the Marattiaceæ. He found points of resemblance to various genera of the family and came to the conclusion that in the whole structure of the sorus it was most like *Marattia*, though in the circular grouping of the sporangia it approached *Kaulfussia*,† and in their partial freedom recalled *Angiopteris*. It has been pointed out that the presence of a pedicel suggests a special comparison with the section *Eupodium* of the genus *Marattia* (*M. Kaulfussii*). Strasburger, however, remarked that in the distribution of the sori on the leaf, *Scolecopteris* differed from all recent Marattiaceæ.‡

Geinitz and Drude simply accepted Strasburger's reference to the Marattiaceæ. The same view is adopted in general works, notably by Professor Bower in his recent important treatise on the Ferns. Speaking of *Scolecopteris*, in particular, he says : ' The Marattiaceous character of this fructification is unmistakable ' (Bower, 1926, p. 114).

Yet the agreement on the question is by no means universal. Dr. Hoskins, in his account of his new species, *S. minor*, after recognising the evidence of the *Psaronius* stems in favour of the Fern-affinities of Pecopterid fronds, concludes, ' In view of the close relationship between the *Asterotheca* and *Scolecopteris* type of fructification, however, conclusive evidence that the plant on which the *Asterotheca* type of sporangia occurs also bore seeds, as indicated by Halle's investigations, would seem to warrant the assumption that *Scolecopteris* likewise is the male fructification of a member of the Cycadofilicales, conclusive

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† Now often called *Christensenia*.

‡ In *Scolecopteris* and its fossil allies, the synangia are ranged in two rows, one row on each side of the midrib of the pinnule ; in recent Marattiaceæ (except *Kaulfussia*, where they are scattered irregularly) they are ranged on either side of a *lateral* vein of the pinna. Prof. Bower (1926, p. 113) states that the arrangement is the same in both groups, but this is only the case on the assumption that the lateral veins in the recent genera represent the pinnule-midribs of the fossils. The fronds of the fossil Pecopterids were generally much more finely divided than those of living Marattiaceæ.

evidence of which, however, must await further investigation ' (Hoskins, 1926, p. 436).

Dr. Hoskins was referring to the discovery by Professor Halle, in the Permian of China, of *Pecopteris Wongii*, one specimen bearing a seed-like body, attached to the rachis. Since Dr. Hoskins wrote, Professor Halle has published a full account of the plant (Halle, 1929, p. 5). He thinks there is little doubt as to the morphological nature of the seed-like body, or as to its actual connection with the frond. 'All the same, he reserves his judgment on the question whether this *Pecopteris* was really a Pteridosperm. Detached ' seeds ' were also found in close association with other specimens. The question is especially important because ' *Pecopteris Wongii* is very similar to *P. Miltoni*, which has fructifica-tions of the *Asterotheca* type strongly suggesting Marattiaceous affinities, and has only with considerable hesitation been referred to a separate species ' (Halle, p. 7). The author adds : ' If it is confirmed that *Pecopteris Wongii* bore seeds, this would afford the definite proof that these genera [*Scolecopteris* among others] are not Ferns and in that case the whole genus *Pecopteris* may be suspected to belong to the Pteridospermæ.'

Thus the Chinese species, if only its nature were certain, would afford the strongest confirmation of the conclusion arrived at by the late Dr. Kidston at the close of his life, when he said that the affinities of *Acitheca* appeared to him to be Pteridospermous, and if so he could not see on what grounds *Astero-theca* and *Scolecopteris* coudl be excluded from the same group, and added : ' It would therefore appear that the evidence in support of the occurrence of Marattiaceous Ferns in Carboniferous times rests on supposition rather than on satisfactory proof ' (Kidston, 1925, p. 538).

The argument which chiefly influenced Dr. Kidston was the similarity of the synangia of the supposed fossil Marratiaceæ to those of *Telangium*, believed on good grounds to constitute the male organs of undoubted Pteridosperms.

This is not the place to enter on a full discussion of this important question. I have dealt with it in a tentative manner elsewhere (Scott, 1929). I will only say here that the detailed examination of the new species of *Scolecopteris* has shown nothing whatever inconsistent with its being a true Fern, having most in common with the Marattiaceæ, nor revealed anything suggestive of an affinity with seed-plants. The resemblance to *Telangium*, a fructification borne on a long naked stalk, seems to me much more remote than that to the synangia of recent Marattiaceæ. The consideration of the vegetative organs in the forthcoming paper by Professor Holden and myself may afford further data for discussion.

I am indebted to Professor Holden for most of the photographs illustrating the present paper, as well as for text-fig. 2.

ADDENDUM

Notes added April 25th, 1931.

Since writing the paper, I have received on loan, from the Geologisch-Paläontologisches Institut of the University of Jena, the original specimens of *Scolecopterus elegans*, Zenker. I am greatly indebted to Dr. K. Mägdefrau and to the Director of the Institute for this valuable loan.

One specimen is the polished plate on which Zenker founded the genus and species in 1837. The plate is accompanied by a coloured drawing, natural size, showing the plate larger than it now is. Evidently a portion had been removed later to provide Strasburger's ' Dünnschliff.'

Under a simple microscope the morphology, though not, of course, the cellular structure, is beautifully shown. Four sporangia in a synangium is the commonest number ; five are frequent, and in one case I noticed six. Practically all the leaflets present are fertile, contrary to what is found in *S. Oliveri*.

The section on which Strasburger worked in 1874 consists of two not very thin slices, mounted without a cover-slip. It is a poor preparation, compared with modern sections, and one can only wonder that Strasburger made out so much. Measurements give about the same results as were obtained from Strasburger's figures.

Height of synangium . . . . 1·0–1·1 mm.

Average height of a sporangium . . . . 0·9 mm.

Maximum width of sporangium . . . . . . 0·32–0·35 mm.

Thus all the dimensions are much smaller than in our species (see p. 4). It appears clear that the two species are distinct.

I have also seen five excellent additional sections of *S. Oliveri*, prepared as before by Mr. Hemingway. The chief point to note is that synangia with only three sporangia certainly occur, while the number five was again observed.—D. H. Scott.

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EXPLANATION OF THE PLATES

(Figs. 2, 3, and 6 are from photographs by Mr. W. Tams of Cambridge ; all the rest by Prof. H. S. Holden.)

PLATE 1.

Fig. 1. Line of fertile pinnules interrupted by the rachis of the pinna in obliquely transverse section. Opposite the rachis is a good transverse section of a sterile pinnule. Slide 148.3, × about 12.

Fig. 2. Part of a line of fertile pinnules, three of which are in approximately transverse section. Subtending sterile leaflets are seen below. Slide 148.4, × about 10.

Fig. 3. Single fertile pinnule from same section, showing two synangia on the under side. The pedicel is well seen on the right. All the sporangia contain spores. The midrib of the pinnule bears a uniseriate hair. Slide 148.4, × about 30.

Fig. 4. Fertile and sterile leaflet in transverse section. The fertile one shows two synangia and its tissues are partly preserved, showing the palisade-tissue, deeply sunk, with hypoderma above. In the sterile pinnule a hydathode is well shown at each margin. Slide 148.5, × about 15.

Fig. 5. Fertile pinnule, bearing two synangia. On the right the pedicel is very well shown. Also the wall of one of the sporangia. Slide 148.2, × about 40.

Fig. 6. Superficial section of fertile pinnule, showing several synangia in horizontal section. In two there are obviously four loculi, in another apparently three. In the upper part of the figure two synangia are shown in apical view. *Cf.* text-fig. 1. Slide 148.1, × about 15.

Fig. 7. Two synangia in horizontal section. One has four loculi, the other five, cut at unequal levels, owing to obliquity of section. Slide 148.6, × about 30.

PLATE 2.

Fig. 8. Synangium in vertical section, showing the pedicel, with its core of tracheal elements. The sporangia appear to be separate, but the section is not perfectly median. Another sporangium shown contains spores. Slide 148.6, × about 40.

Fig. 9. Another synangium in vertical section, showing the tracheal core of the pedicel and its connection with the sporangial walls. Slide 148.4, × about 40.

Fig. 10. Synangium in tangential vertical section, showing the tracheal core of the pedicel, and the sporangial walls in surface-view. Slide 148.3, × about 40.

Fig. 11. Tracheal core of pedicel from the same section, showing the reticulate sculpturing on the cell-walls. Slide 148.3, × about 150.

Fig. 12. Tracheal core of pedicel shown in fig. 3. The cells at the base are elongated, indicating the junction with a vein of the pinnule. Slide 148.4, × about 210.

Fig. 13. Synangium in vertical section, to show the slight basal cohesion of the sporangia. The midrib of the pinnule is conspicuous on the left.   Slide 148.5, × about 40.
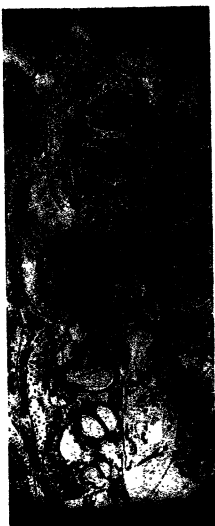
SCOLECOPTERIS OLIVERI, SP. NOV.

Holden phot.

SCOLECOPTERIS OLIVERI, SP. NOV.

Tams and Holden phot.

Some New Zealand indigenous-induced weeds and indigenous-induced modified
and mixed plant-communities. By L. COCKAYNE, C.M.G., Ph.D., F.R.S.,
F.L.S., G. SIMPSON, F.L.S., and J. SCOTT THOMSON, F.L.S., F.C.S.

'(PLATES 3–7)

(Read 16 April 1931)

I. INTRODUCTION

The vascular flora of New Zealand, according to the most recent estimate,
consists of 1850 indigenous species—including a few exceedingly distinct
varieties, 427 groups of species-hybrids, a large number of varietal hybrids
(those within compound species), and about 650 exotic species. Owing to the
unavoidable destruction for economic purposes of extensive areas of the
vegetation (chiefly replacing forest by artificial grassland and ploughing
suitable ground), and the exploitation and consequent modification of various
plant-formations, particularly tussock-grassland and rain-forest proper,*
great changes have been wrought in the structure and the relative abundance
of the species of a plant-covering until recently primeval, while also its area
of occupation has been greatly reduced. Such changes, too, have been
accelerated by the deliberate or accidental burning of many different plant-
communities and the introduction into the virgin vegetation of a good many
species of grazing and browsing animals, some rightly brought into the Region
for economic reasons, but others entirely for purposes of sport. To this last
class must be added those domestic animals—no mean number—which have
become feral, the first of such being the pigs let loose by Captain Cook.

These extensive changes in the vegetation which have taken place, and are
still in active progress, afford material of particular interest for study, especially
as the flora and vegetation came into being in the absence of grazing and
browsing mammals—an extremely rare occurrence elsewhere. Thus, the plants
were brought face to face with a novel destructive element, to counter which they
were ill-equipped. As for fire, where hot ashes, or molten lava, set vegetation
ablaze, the happening was just as natural as that caused by any other primary
factor, so that what takes place at the present time in an area dominated by
extinct volcanoes (burning *Nothofagus* forest, for example) can hardly be dis-
similar from what happened, again and again, in the days of volcanic activity—
the main difference being that now a combination of indigenous and exotic
plants may form the new community, as in the eruption of Mount Tarawera
in 1886. So, too, the destruction of upland forest by avalanches comes into the

* An abbreviation of subtropical rain-forest.

same category as one felled by axe and cross-cut saw. Further, consideration of the examples given in this paper, with those published in ' The Vegetation of New Zealand,' ed. 2, should have some bearing on what happened long ago in lands (e.g. Europe in general), even then under the partial domination of man, where now virtually all the plant-covering is no longer primeval, but probably greatly altered, though some is frequently described as ' virgin '. No New Zealand plant-ecologist of wide experience could be misled in this direction, for he would know from comparative studies how an apparently trivial attack made by man on a virgin plant-community may obliterate its primitive stamp, yet, to the uninitiated, it will look primitive enough.

In ' The Vegetation of New Zealand ', ed. 2 (Cockayne, L., 1928, pp. 352–77), part iii is entitled ' The effect of settlement upon the Plant-covering of New Zealand ', and one of its chapters is devoted to the new vegetation. Of necessity, many ' new ' communities receive no mention, and, in part, this paper is intended to fill that gap. In addition, however, the occurrence of indigenous plants as ' weeds ' receives consideration, since, not only is the subject of general interest, but the spread of the individual plant beyond its original limits forms an indispensable basis for considering the origin, structure, and composition of the new communities.

In the above-mentioned work the vegetation is divided into several classes, and to these we add another—the ' mixed '. These various classes we define as follows : (1) PRIMITIVE, that which is truly virgin : (2) MODIFIED, that which is more or less altered but not so greatly as to change the primitive stamp ; (3) INDUCED, when a new community, either unknown in primeval nature or one apparently identical with a primitive community, has been brought into being by the direct or indirect influence of man. This class falls naturally into (a) Exotic-induced, when the community consists entirely, or principally, of exotic species ; (b) Indigenous-induced, when the community consists, entirely or principally, of indigenous species ; (c) Mixed, when the two classes of species occupy about an equal position in the community ; and (d) Artificial, when the community has been made by any method of cultivation, including the felling and burning of forest and sowing seeds of pasture plants on the ashes (' bush-burning ', a ' bush-burn ').

Contrary to the statement made so frequently by distinguished biologists that in the struggle between the indigenous and exotic plants in New Zealand the latter are invariably the victors, time after time, since 1900, have New Zealand botanists shown this to be a mischievous fallacy. Yet even a New Zealand writer, so recently as 1919 (Herriott, E. M., p. 446), wrote : ' The *fact* [italics ours] that our native flora does disappear before European plants has been recorded more than once . . . the practice of burning large tracts of vegetation destroyed many of the natives and the native flora had no plants which could take possession of fresh soil laid bare in any of these ways ' —attacks of introduced animals, burning, &c. Yet in spite of this apparent adherence to a worn-out creed, the author shows that there still remain in

Hagley Park (part of the city of Christchurch) no less than thirty-eight species (and there are certainly more) out of the eighty-eight of 1864, notwithstanding the constant use of the area for heavy grazing and playing-fields, and the filling in of a large swamp ; indeed, few facts could better illustrate the staying-power of indigenous species under particularly hostile circumstances, and this is fully recognised by Miss Herriott herself, for she writes (l.c. p. 446) ' it is astonishing not that we have so few native plants in our Park but that we have so many '.

It is not surprising that the earlier naturalists, e.g. J. D. Hooker, T. W. L. Travers, and even T. Kirk and T. F. Cheeseman, were amazed at the manner in which many members of the exotic flora had spread and were spreading, and that the extravagant statements made as to the impotence of the native plants to compete against the foreigners, such as white clover and cat's-ear, were not considered far-fetched. Even now, hill-sides a blaze of gorse and broom, and road-sides for miles a continuous thicket of blackberry, cannot fail to make the visiting botanist feel that the exotic species are all-powerful. Such an one motoring amongst hills clad with an apparently uniform grass-covering would feel rather sceptical when informed that the hills only a few years previously were densely forest-clad, but that the forest had been felled, its members burned, and the exposed ground converted into the equivalent of a European pasture by sowing seeds of foreign grasses and leguminous plants ; while, on the other hand, what he now saw was a European meadow no longer, but one where the indigenous grass, *Danthonia pilosa*, unaided directly by man, had become dominant.

In order to view the relation between the exotic and indigenous floras in their proper perspective, certain fundamental differences between the two in their life-forms, their habitat-preferences, and their altitudinal distribution must be stressed. This done, it will be seen that, in no few instances, competition between the two floras is virtually absent. Further, it must not be forgotten that rarely is there competition between the exotic and the indigenous, but that the former is greatly aided by man* through his direct action and that of his fires and his introduced wild and domestic mammals. For example, where the upland sheep-pastures in various parts of South Island abut suddenly upon an area where there have been neither sheep nor burning, this is still clad with its pristine plant-covering with *all exotics absent*,† so that the surprising difference between the two areas stands clearly revealed. Again, paths have been made on certain mountains in the subalpine belt, and on such various exotics may be established, yet these have not gained a footing in the virgin communities which border such paths.

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* It was this neglect to appreciate man's part which made the writers cited above exaggerate the role of the exotic in displacing and replacing the indigene ; neither did they view the matter from the ecological standpoint.

† Year by year, areas where exotic grazing and browsing animals have not penetrated become fewer and fewer, i.e. primeval New Zealand is rapidly disappearing.

There is no need to labour this part of our subject, since the general aspect of the case, based on personal observations made in typical parts of nearly the whole Region, has been stated by L. Cockayne as follows : ' wherever any part of New Zealand is in its primitive condition and uninterfered with by man or the animals he has introduced, none of the exotics have gained a foothold, their great powers of dissemination notwithstanding, although the virgin area may be pierced in all directions by ground occupied by man where there are introduced species in plenty '.* That is to say, no exotic can gain entrance to a piece of virgin vegetation until such is broken up. To this statement there are one or two apparent exceptions. Thus in the *Leptospermum* shrubland of the Auckland Districts the Australian *Hakea acicularis*, of a somewhat similar life-form to *L. Scoparium* is common, but probably its entry into the association was aided by burning. So, too, *Hakea saligna*, originally purposely sown, occupies a wide area on boggy ground near Collingwood (North-Western District), along with *L. Scoparium*; and a Mediterranean species of *Erica* has become very common in stunted *L. Scoparium* and bracken in the South Auckland District.

As already stated, the exotic vascular species for the Region number about 650, less than one-third of the indigenous species, 1850. Nevertheless, since the exotics with but few exceptions are confined to the lowland and montane belts, and as the number of indigenous species for those areas in North Island and South Island does not greatly exceed 1,000, the discrepancy between the two opposing bands is greatly lessened.

Far more important than their relative numbers is their equipment for the fray. This is clearly reflected by their life-forms, so different in the two classes and each fitted for equally different sets of conditions. Thus, the exotics for the most part are annuals, occasionally biennials, in form unlike nearly all the indigenous species, usually producing a much greater number of seeds, with more rapid germinating power and probably greater viability. As for their habitats, the exotics affect cultivated ground and such as has been laid bare in the process of settlement—they are, as it were, the companions of man. On the other hand, the indigenous plants are in large part woody or semi-woody evergreen perennials ; true herbaceous summergreen † herbs occur principally in the high mountain flora, but, even there, are in a great minority, and annuals and biennials are almost negligible in all the altitudinal belts.

As for the edaphic habitats, these are an unbroken soil. Even in the greatly exploited lowland-montane low tussock-grasslands of South Island, where the indigenous species number about 216 and the exotic species about 74, many

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* Cheeseman's premature statement ' there is no corner, remote and apparently inaccessible though it may be, into which some of these species of northern origin [most of the exotics of this paper are] have not found their way and thrust out a portion of the original possessors of the soil ' (1883, pp. 268–69) ; owing to observations made, since he wrote. in virtually all parts of the main and outlying islands this is now known to be incorrect.

† We make one word of this, as in the case of ' evergreen ',

of the latter are confined to bare places (sheep-tracks, road-sides, broken ground, &c.) and can be considered temporary invaders rather than true colonists. The latter, so far as importance goes, are but few, particularly noticeable being *Agrostis alba* (in a wide sense), *Anthoxanthum odoratum*, and *Hypochaeris radicata*—which Travers stated to have destroyed excellent * pasture in three years and ' which absolutely displaced every other plant on the ground ' † ; but this species is no more aggressive, or persistent, on low montane tussock-grassland than is *Plantago spathulata* of somewhat similar life-form. Where fenced from stock and rabbits, exotics notwithstanding, should the climate not be too dry, the indigenous species of the above community rapidly increase. Even on ground laid bare by rabbits in the lower subalpine belt of the North-Eastern District, heavily manured by them and pierced by their holes, the following five indigenous and two exotics may be common :—*Carex breviculmis, Rumex Acetosella, Cerastium vulgare, Geranium sessiliflorum* var. *glabrum, Acaena Sanguisorbae* var. *pilosa, Epilobium novae-zelandiae,* and *Raoulia lutescens*.

Unless the contrary be stated, the data presented in this paper are taken from notes made by ourselves, working either singly or conjointly.

We must thank most sincerely the following for valuable assistance in various directions : Miss Lucy M. Cranwell, M.A. (Auckland), Dr. W. McKay (Grey-mouth), Messrs. A. C. B. Thomson (North Taieri), and J. B. Thomson (Inver-cargill).

II. INDIGENOUS-INDUCED WEEDS

(a) GENERAL.

In regard to what follows, we define a ' weed ' as a plant occurring in an economic plant-community—' economic ' being used in a wide sense—which in any way is harmful to the well-being of the community. Of course, in a virgin vegetation there can be no weeds in the above signification, a plant being a weed only in its relation to man, though, even in primitive nature, a particular plant may become far more abundant than usual, as does the small deciduous tree *Hoheria glabrata* in subalpine or montane forest where the stony ground is left bare by avalanches or such ground is provided by land-slips. A rather unusual example of this kind is to be seen on Antipodes Island, where the young albatross, paddling on the peaty ground round the nest it has occupied so long, lays bare the peat, which, the bird having taken to the sea, is soon colonized by the delicate creeping *Stellaria decipiens* var. *minor*, and the far more aggressive *Acaena Sanguisorbae* var. *minor*.

This matter of indigenous weeds is particularly important in that it shows the evolution of this world-wide class of plants, for the origin of the weed-host

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* Experiments, coupled with hundreds of observations, have proved that this plant comes into the first class so far as palatability for sheep is concerned.

† Wallace, 1889, p. 29.

of temperate lands in general is wrapped in obscurity, any potential weed in a primitive vegetation occupying a definite position and being no more aggressive than its fellows, though an alteration in habitat-conditions frequently leads to increase in numbers of certain species, i.e. a new succession may be rapidly developing.

In pre-European New Zealand, weeds, either exotic or indigenous, were unknown. Further, it is nearly always known whether a species is indigenous or not, and, if indigenous, what its relative position is in regard to other species in the virgin vegetation. Here, then, an absorbing study lies to hand concerning the indigenous-induced weeds and one which, though far from being exhausted, has already yielded interesting results, some of which are briefly dealt with below.

If the question of aggressiveness be considered, it must be emphatically declared that there are no weeds in the exotic flora which can vie either with the bracken fern (*Pteridium esculentum*) or that great mixture of varietal, &c., hybrids known as *Leptospermum Scoparium* ; but, no matter how aggressive any species and band of such may be, the latter is merely an early succession kept from progressive change principally by grazing, burning, and agricultural operations. Were all stock removed from North Island and South Island and the pastures and cultivated ground let alone, it seems certain that in one hundred years' time various stages of forest-development would occupy the land, the close sward of exotic grasses, &c., notwithstanding. Such forest would be principally rain-forest, yet where there are areas of *Leptospermum* shrubland in the vicinity of exotic conifers or *Eucalypti*, forests of these would also become established— either pure, or mixed with indigenous forest-plants.

(b) GRASSLAND WEEDS.

(1) THE SPECIES OF C A S S I N I A (COMPOSITAE).—There are six species, all moderate-sized, much-branched, ericoid shrubs, one of which (*C. amoena*) is confined to the very small North Cape Peninsula and so of no moment here, but the remainder and their very large groups of hybrids are excessively aggressive. In primitive New Zealand, *Cassinia retorta*, *C. leptophylla*, and *C. fulvida* (in a limited sense) were essentially coastal species, confined to dune, rock, mixed shrubland, &c. At the present time, *C. leptophylla*, more or less *C. fulvida*, and their numerous hybrids,* form close low thickets on those artificial or indigenous-induced pastures with which farming has replaced semi-coastal forest in the Ruahine-Cook and the Sounds-Nelson Botanical Districts, and in certain localities such thickets extend for some miles inland. European grasses and clovers are powerless to overcome them ; if burned, they rapidly regenerate from seed, and to attempt their eradication the shrubs must be

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* Here, and in all other cases, the individuals of a hybrid group are alone called hybrids, while the group itself is expressed by a formula and may in addition bear a binomial name, but it (the group) is certainly not a hybrid,

pulled up, but unfortunately the disturbed ground is specially favourable for germination of their seeds.*   In the montane and lower subalpine belts of certain parts of the eastern ranges and adjacent valleys of South Island, *C. albida*, restricted to the Sounds-Nelson and North-eastern botanical districts, *C. Vauvilliersii*, *C. fulvida* var. *montana*, and the hosts of hybrids between the two or the three species, are greatly in evidence on tussock-grassland opened out by repeated burnings, as also in neglected cultivated fields.

(2) C O R I A R I A   S A R M E N T O S A (CORIARIACEAE).—In modified lowland-montane low tussock-grassland of South Island far-spreading bushes, up to about 80 cm. high, of this summergreen, almost woody plant invade shady slopes where the soil is more or less moist and form such extensive colonies in places as almost to rank locally with those of *Pteridium esculentum*.   Fire is harmless to the well-being of this species, thanks to its far-extending stout underground stems, but continuous grazing by sheep wipes it out, these animals apparently becoming immune to its active poison.   The allied small tree, *C arborea*, is frequently aggressive on the margin of lowland forest.   The smaller species *C. lurida*, *C. angustissima*, and the many hybrids between the two, and *C. sarmentosa*, may occur in large quantities in montane-subalpine grazing land where the rainfall is excessive ;   they also appear in abundance where subalpine forest has been felled.

Originally, *Coriaria sarmentosa* and its smaller allies would be rare, or absent, where now abundant, and confined to shrubland, rock, stony river-bed, fell-field, and herb-field.   In the man-made steppe (Cockayne, L., 1928, pp. 363–65), *C. sarmentosa*, perhaps the most remarkable of all indigenous-induced vegetation, fringes the water-races made by the gold-diggers, but now used for irrigating orchards and fields of lucerne.

(3) SPECIES AND HYBRIDS OF A C A E N A (ROSACEAE).—In this case the farmer, who ignores the insidious advances of most weeds, is fully aware that the presence of hutuwai, piripiri, and biddy-bid (vernacular names for the species, &c., of *Acaena* in general) is a serious menace to his pastures, and the burrs (fruits) highly damaging to his wool.   Indeed, national attention has been called to the danger, and an attempt is now being made to reduce the evil to a minimum through the establishing of some ' natural enemy ', such being looked for in southern South America.   Even if such an insect be forthcoming, it is hardly likely to attack all the ' forms '† equally and indiscriminately, and it is possible that such selective feeding might preserve and further the increase of some particularly virulent variety.

The New Zealand species of *Acaena* number at least ten groups of more or

* So, too, pulling up the exotic *Digitalis purpurea* only assists in increasing this aggressive weed.

† We use the term ' form ' to designate any individual or group within a species, the exact status of which is unknown, and have found this application of the term exceedingly useful.

less diverse individuals, but the so-called 'varieties' referred to the great linneon,* *A. Sanguisorbae* Vahl, are really so distinct from one another that they might well be treated as separate compound species,† were it not that so doing would veil their close relationship. These varieties cross freely with one another, except var. *viridior*, and some of them with the very distinct *A. microphylla*, *A. inermis*, *A. glabra*, and even the exotic *A. ovina* (Australian). All the species, &c., except *A. ovina*, have far-creeping, semi-woody, rooting stems which form large circular mats. The calyces, except in *A. microphylla*, *A. inermis*, and *A. glabra*, bear rather long, barbed spines, and these still persist with enhanced clinging power on the hardened calyx which surrounds the achene. Anyone walking through a plant-community where such Acaenas are abundant, and where, perhaps, for hectare after hectare there is little else, will soon have trousers or stockings covered deeply, even to the knees, with a tenacious brown covering difficult to remove. In primitive New Zealand, distribution of the achenes would be principally by the ground-birds,‡ but now in pastoral areas various animals, particularly sheep and dogs, spread the seeds far and wide.

In the existing virgin plant-communities *Acaena* rarely, if ever, dominates, for it is held in check by its associated plants, but, once bare ground is provided, either by natural or artificial means, its numbers increase tenfold. If nature works unhindered, the mats act as seed-beds and the Acaenas will be overpowered by the plants they nurture, some of them eventually dense shrubs which cut off the light, others powerful tussocks, close mats, and so on. On pasture grazed by sheep it is otherwise, for the competing grasses, &c., eaten by these animals are kept in check, but the unpalatable Acaenas increase rapidly. Possibly, too, the numerous hybrids possess even greater vigour than their extremely vigorous parents, if such be possible. Another advantage possessed by members of the *Sanguisorbæ* group (this includes also *A. novae-zelandiae* T. Kirk) is their lianoid habit when growing amongst taller plants.

(4) HISTIOPTERIS INCISA AND PAESIA SCABERULA (FILICES).— In order to attain success during the establishment of permanent pasture after a 'bush-burn' the area must be fully stocked (sheep on the poorer hilly country, cattle on the richer flat land), the trampling of the animals leading

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* This term is here used not in Lotsy's meaning as a Linnean species, but in that of Cockayne and Allan, as a polymorphic group consisting of more than one species together with the hybrids between them, their varietal hybrids, and their epharmones (habitat-forms, modifications).

† *Compound species* are those made up of two or more extremely closely-related apparently true-breeding groups of virtually similar individuals (jordanons). *Simple species* consist of merely one jordanon which is not clearly related to any other. Epharmones are, of course, included in species. *Varieties* are such jordanons of a compound species as are sufficiently distinct to admit of effective diagnosis.

‡ On the Subantarctic Islands young albatrosses on their journey to the sea, being unable to rise from the ground, spread *Acaena Sanguisorbae* var. *minor* far and wide Cockayne, L., 1909, pp. 234–45).

to a sward, and this and their grazing to the destruction of seedlings of forest-plants, &c. At first, in any case, many fallen tree-trunks cumber the ground and assist in providing too much shade and in protecting those indigenous plants ('weeds) which soon come in and are not wanted in the pasture. Of such, the far-creeping ferns, *Histiopteris incisa* and *Paesia scaberula* are frequently extremely troublesome—the former in moist shady situations, hence the farmers' name ' water-fern ', and the latter where drier. Both species are absent in forest except where considerable light has been let in. A partial or insufficient burn favours the incoming of still worse indigenous weeds, e.g. *Pteridium*, *Aristotelia serrata*, *Leptospermum Scoparium*, and, near the coast, *Cassinia*. Also, at times, the ' burn ' is unsuccessful and most of the forest trees and shrubs return. Whether or not such indigenous-induced forest truly represents the original or any other primitive community we do not know.

(5) RUMEX FLEXUOSUS, ETC.—On bush-burn, sown pastures, or those ploughed after the burn, in the wet climate of Westland (more than 250 cm. of rain yearly) certain indigenous species occur which are absent, or, at best, extremely rare in those of drier localities. Perhaps the most conspicuous of these induced seeds are the brown- or green-leaved varieties of *Rumex flexuosus* which form irregular mats. This species is not found in forest, but in Westland is apparently a plant of wettish places on river terrace and the like. In addition, other rhizomatous or stoloniferous plants may also be present, e.g. (on unploughed ground) *Histiopteris incisa* and *Paesia scaberula* and (on ploughed ground) *Hydrocotyle novae-zelandiae* (or it may be *H. americana*) and *Pratia angulata*. In such pasture, regularly grazed by cattle, about half the sward may consist of indigenous species. Doubtless other indigenous weeds occur, but our notes on these are insufficient.

(6) OTHER GRASSLAND WEEDS.—There are other more or less important grassland indigenous weeds which have been described elsewhere, e.g. *Celmisia spectabilis*, *Chrysobactron Hookeri*, *Lycopodium fastigiatum* (very local), and others for which we have no space for discussion, e.g. *Phormium tenax*, *Arundo conspicua*, *Danthonia pilosa* (dealt with under another heading), *Muehlenbeckia complexa*, *Pimelea prostrata*, species of *Aciphylla* (dealt with under another heading), *Oxalis corniculata*, and other small, vegetatively-spreading herbs.

We must, however, lay stress on the fact that, as far as we can gather, indigenous weeds are altogether absent (excepting species of *Juncus*) in artificial pasture of a high class, this being largely due to the dense sward, the practice of top-dressing with artificial fertilizers, good drainage, constant heavy grazing, and, usually, the considerable distance from any indigenous plant-community. This last factor must always be remembered since, even in primitive New Zealand, it was rather that the plant-community moved as a whole, than that its members were spread far and wide by means of disseminules.* This statement, too, holds good in general for exotics, and their presence frequently

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* This matter is gone into in some detail by L. Cockayne (1928, pp. 73, 74, 143, 247).

depends not upon seed having spread from one centre, but from seed of the exotic in question having purposely, or accidentally, been sown again and again in places far distant from one another.

(c) FOREST WEEDS.

(1) GENERAL.—Strictly speaking, in virgin, or even artificial forest, any members of the community which, in one way or another, interfere with its economic development are 'weeds', but this class receives no consideration here. On the other hand, species deleterious to sylviculture *already in the community*, which increase their area of occupation, are weeds just as much as those which enter from the outside, be they exotic (*Rubus fruticosus, Sambucus nigra, Hypericum Androsaemum,* * &c.) or indigenous (*Pteridium esculentum, Histiopteris incisa,* &c.).

In indigenous forests, the chief causes of the spread or entry of objectionable plants are the letting in of abundant light and such as, in any way, lead to the making of bare ground. Bare ground also arises naturally on a large scale through land-slips, avalanches, volcanic fires, the destruction of areas of adult trees in various ways (old age, unusually high winds, diseases, &c.). In artificial forest (of which there are now about 17,344 hectares) some of the trees themselves, if not sufficiently thinned, are weeds, and so are plants of the undergrowth which enter in and are a hindrance to natural regeneration, should this be desired, or have to be removed, if replanting after 'clear felling' is to be undertaken.

In addition to forest-weeds proper are those in the various types of forest set aside as Monuments of Nature—'Scenic Reserves' is the Dominion title.†

A weed of millable forest ‡ is primarily one hindering the establishment of seedlings of the timber trees and their proper development ; and so even exotic weeds, when few in number, or of poor spreading power, may be negligible. On the contrary, in a Scenic Reserve, any indigenous or exotic plant which does not properly belong to the community is a weed. The exotic weeds are usually of but little moment, but they may occur in quantity and defeat the ends of the reserve, especially gorse, broom, blackberry, elderberry, tutsan, *Leycesteria formosa* ; and in North Island, on the forest's outskirts, the lianoid *Senecio mikanoides.* To introduce indigenous species which do not belong to a Scenic Reserve is a desecration, but unfortuantely this is not generally understood and such action is considered laudable by some !

(2) THE ENTRY OF VARIOUS CLOSE-GROWING, DENSE, SHADE-PROVIDING PLANTS, OR INCREASE IN THE AREA THEY OCCUPY.

(α) *Tree-ferns and semi-tree-ferns.*—Frequently tree-ferns form close colonies

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* None of these can enter virgin forest, the degree of light of its interior being always too weak.

† Scenic Reserves also include other types of scenery, as also places of historic interest.

‡ Forest which contains sufficient trees for converting into timber.

within which little, if anything, can grow. In *Dicksonia squarrosa* and the extremely slender *Blechnum Fraseri* (of low stature) the increase of individuals is due to stolons* which, given off from near the base of the trunk, spread in all directions beneath the ground and give rise to new individuals. The case of *B. Fraseri* was first described by L. Cockayne (1908, pp. 14, 15), who showed that it increased greatly with increase of light. Perhaps more interesting is the fact, discovered recently by Mr. P. Black (Director of Parks and Reserves, Palmerston North), but not published hitherto, that the extensive colonies of the medium-sized tree-fern, *Dicksonia squarrosa*, so common throughout all New Zealand proper, are due to vegetative increase by means of stout stolons (Pl. **3.** fig. 1). Fire does not check the development of the great colonies, but increases them rather, as may be seen constantly in proceeding from Hokitika to the Franz Josef and Fox Glaciers, or after crossing the Haast Pass. Burning the semi-coastal forest of Chatham Island also led to a dense growth of tree-ferns and little else. The closeness of growth of the individuals, coupled with the light-obstructing lie of the large fronds, makes the establishment of seedlings, &c., within the fern colony virtually impossible (Pl. **3.** fig. 2). In *Hemitelia Smithii*, which also forms groups of considerable size, stolons are wanting, and for the remaining tree-ferns we have not as yet made sufficient investigations.

Blechnum discolor, which also has the stoloniferous habit (Pl. **4.** fig. 3) is probably the most serious obstacle to regeneration in the indigenous forests. It forms far-extending colonies (Pl. **4.** fig. 4), each plant bearing on a short trunk an open crown of leaves ± 90 cm. in diameter. Such a close-growing, far-extending, deep floor-covering forbids the establishment of seedlings, both of economic and non-economic trees, and of all other undergrowth. *Blechnum fluviatile, B. lanceolatum, B. Patersoni, B. vulcanicum,* and *B. procerum* likewise form colonies vegetatively.

Polystichum vestitum also occupies wide areas, especially of the floor of subalpine forests, but its spreading is due, not to stolons, but to rapid propagation by spores, and its shade-producing property to its excessive branching from its short trunk and close crown of leaves. The great abundance of *Leptopteris superba* is apparently not due to stolons, but we suspect that the trunkless form of *Dicksonia lanata*, so abundant in mountain forests of Central North Island, is stoloniferous.

(*β*) *The presence or incoming of shrubs and other plants of dense habit.*—Shrubs of the divaricating life-form (many species of *Coprosma, Suttonia divaricata,* juvenile *Pennantia corymbosa, Plagianthus betulinus,* and *Melicope simplex*), plants of the tussock-form (species of *Gahnia,* juvenile *Cordyline indivisa*), and any plant which rises above the substratum and cuts off the light are hostile to sylviculture. In North Island semi-swamp forest, when most of the trees of *Podocarpus dacrydioides* are removed, a dense growth of divaricating shrubs

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* We give this name provisionally to the branching underground stems, for we have not studied them sufficiently to be sure of their morphological status.

may forbid tree-regeneration.   So, too, open spaces in kauri forest occupied by the great close tussocks of *Astelia trinerva*, and especially *Gahnia xantho-carpa*, are veritable huge beds of weeds.   It is the rather similar life-form of juvenile *Cordyline indivisa* which secures the temporary dominance of that plant, its seeds also being highly viable, in certain North Island upper montane forests after the tall trees have been felled or burned.   To the north of lat. 42° S. *Myrtus bullata* of dense habit, and × *M. bullobcordata* (if *M. obcordata* is present), in many places where light has been let into the forest, form tall close thickets inimical to the seedlings.

(3) INDIGENOUS SHRUBS, ETC., INVADING PLANTED ARTIFICIAL FORESTS OF EXOTIC TREES.—Near Rotorua (Volcanic Plateau District) certain plantations of exotic trees (now about thirty years old) were made by H. J. Matthews, then ably directing forestry operations for the Department of Lands and Survey. In February 1928, in a *Eucalyptus* plantation, L. Cockayne noted that there was an undergrowth of *Pteridium esculentum* (1·8 m. to 2·4 m. high), under which, where densest (its greater part), there were no plants, but where a fair amount of light came in there were a few plants of the indigenous trees or shrubs, *Notho-panax arboreum* (Pl. **5.** fig. 5), *Dodonaea viscosa*, *Pittosporum tenuifolium*, *Gaultheria antipoda*, *Leucopogon fasciculatus*, and the herbaceous *Dianella intermedia* and *Pratia angulata*.   The sole exotics were a few seedlings of *Berberis Darwinii* and of the *Eucalyptus*.

In a plantation of *Larix decidua*, where some of the side-branches were not yet suppressed, the ground was bare except for an occasional *Nothopanax arboreum*, but where plenty of light entered, at the junction of the larch and the *Eucalyptus* plantations, there were young trees of *Nothopanax arboreum* (1·5 m. to 2·4 m. high), some *Coprosma robusta* or *C. lucida*, and a small amount of *Pteridium*.

In a plantation originally of *Larix decidua* and *Betula alba*, but with the latter cut out some years ago, there was a far richer undergrowth than in the above plantations, consisting of the following indigenous species :—*Coprosma robusta*, *Geniostoma ligustrifolium*, *Nothopanax arboreum* (up to 2·1 m. high), *Olearia furfuracea*, *Pittosporum tenuifolium*, *P. eugenioides*, *Leucopogon fasci-culatus*, *Gaultheria antipoda*, and one plant or so of *Leptospermum Scoparium* (not sufficient light generally for that species) ; *Pteridium* was absent.   An inter-esting feature of this invasion of artificial forest by indigenous trees and shrubs is that the seeds of all came from plants growing in the adjacent ornamental beds of the nursery and that such had not reached the more distant plantations.

(d) WEEDS OF CULTIVATED GROUND.

Indigenous weeds are virtually absent in arable fields or in gardens.   In the former, on the Canterbury Plain in the early days of settlement, the deep-rooting switch-shrub, *Carmichaelia subulata*, persisted for a few years and that species seems to be about all there was.   The liane, *Muehlenbeckia complexa*,

sometimes still occurs in hedges.* In gardens with indigenous trees, shrubs, or forest in close proximity, various ferns, species of *Coprosma*, *Hebe salicifolia*, and *Cordyline australis*, may appear.   *Cardamine heterophylla*, *Epilobium nummularifolium*, and *Cotula australis* are quite common.   More interesting is the fact that where the climate is suitable a good many herbaceous and semi-woody plants, mostly what are styled ' alpines ', reproduce themselves freely from seed or soon seize upon much ground by their vegetative increase.   Even in Wellington, where ' alpines ' are not easy to establish, quite a number rapidly spread vegetatively and become ' weeds ' in the alpine garden of the Otari Open-air Native Plant Museum, e.g. species of *Acaena*, *Muehlenbeckia axillaris*, *Wahlenbergia Matthewsii* (rock-plant in its natural habitat), *Gunnera Hamiltonii* (extremely rare as a wild plant), *Cotula squalida*, the creeping species of *Epilobium*, *Poa Cockayniana*, *Helichrysum bellidioides*, *H. alpinum*, and species of *Veronica* allied to *V. catarractae*.

In the South Otago District a large majority of the high-mountain species grow with extraordinary vigour, many of them reproducing themselves from seed in great numbers. L. Cockayne's theory that the high-mountain flora originated in the lowlands under subantarctic conditions, but gradually took to the high mountains, since it was unable to compete with the forest and tussock-grassland (1925, pp. 77–80), thus receives some support. In the gardens of J. S. Thomson and G Simpson in Dunedin more than two hundred high-mountain species grow well, a large majority rapidly increasing vegetatively and others producing seedlings in abundance. Amongst the most aggressive vegetatively are the following, here cited in alphabetical order, omitting such as have been already mentioned :—*Aciphylla pinnatifida*, *Blechnum penna-marina*, *Brachycome Sinclairii*, *B. Thomsonii*, *Celmisia holosericea*, various mat-forming species of *Celmisia*, *Claytonia australasica* (an aggressive plant on the shady slopes of the induced steppe of Central Otago), *Coprosma repens*, the mountain species and hybrids of *Coriaria*, several mat- or turf-forming species of *Cotula*, various species of *Epilobium* (also from seed), species and hybrids of *Gaultheria*, species of *Gnaphalium*, the semi-woody species and hybrids of *Helichrysum*, many species and hybrids of *Hebe* (producing seedlings in abundance), the species and hybrids of *Hierochloë*, the species of *Hydrocotyle*, various alpine species of *Luzula*, *Leucogenes grandiceps*, *Leucopogon Fraseri*, *Lobelia linnaeoides*, *Ourisia caespitosa*, the species of *Oxalis*, the species of *Pratia*, various rhizomatous species of *Ranunculus*, mat-forming species of *Raoulia*, *Veronica Bidwillii* (also seeding), *V. Lyallii* (also seeding), *Viola filicaulis*, and *Wahlenbergia albomarginata*.

In addition to the above, at least one hundred and twenty species seed freely in cultivation, but in this estimate some ' alpine-like ' lowland species are included.

* On many roadsides modified low tussock-grassland still remains containing numerous species belonging to that formation, notwithstanding the abundance of exotic species firmly established throughout the area. When in flower *Chrysobactron Hookeri* var. *angustifolia* and *Celmisia longifolia* are conspicuous.

III. INDIGENOUS-INDUCED COMMUNITIES

(a) GENERAL.

Indigenous-induced communities are for the most part successions, but probably differing, more or less, from any primitive successions, although the final stage of their development may to all intents and purposes equal a primitive association. The leading factors which have induced the class of communities under consideration are as follows :—(1) fire lit directly or indirectly by man ; (2) the action of introduced grazing and browsing mammals—domestic and artificially-feral—in feeding on the plants, damaging them in other ways, consolidating the ground by trampling (opening it out in the case of pigs), causing movement of the substratum, manuring, &c. ; (3) removal of parts or the whole of plant-communities ; (4) establishing induced-exotic communities in various ways, which in their turn—man further interfering or the contrary—give place to indigenous-induced or mixed communities ; (5) drainage or making lakes and streams ; and (6) the making of new ground devoid of plant-life, either artificially or by causing land-slips. The new community, according to our treatment of the subject, need not consist of species which have come into the new habitat from without, nor need it have any limitations as to size, so long as it forms a definite recognizable feature of that mosaic which constitutes a larger community. Thus, though much of a community may be virtually virgin, there may be intercalated new minor communities, large or small, made up of species which are members of the virgin community, but frequently play a minor part therein. Other indigenous-induced communities are those of quite bare edaphic habitats, the exact like of which were unknown in primitive New Zealand. These are of particular interest, since it might well be thought that exotics would have seized upon such new ground, Also, in considering any type of induced or mixed vegetation, it must not be forgotten that the species available for colonization are not only the indigenous but also the exotic with their reputedly overwhelming colonizing power. For instance, it was hardly to be expected that the fifty-five species which are now occupying the rock left bare a few years ago by the Franz Josef Glacier, in its lowland and montane portion, would all be indigenous, as they are, notwithstanding the seed-carrying winds which, Mr. A. P. Harper informs us, so frequently blow over the Westland Plain to the Glacier. In the case also of the naturally sterilized deep covering of volcanic ash provided by the eruption of Tarawera in 1886, the species now occupying the ground are chiefly indigenous, while the exotics were mostly purposely sown in order to provide pasture.

In ' The Vegetation of New Zealand ', ed. 2, the particularly striking indigenous-induced communities are described at some length, but generally too briefly.* Here, anything said about them is merely supplementary.

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* The following are dealt with :—*Danthonia pilosa* grassland, Induced steppe of Central Otago, Colonies of *Celmisia spectabilis* and *Chrysobactron*, the incoming of *Lycopodium fastigiatum* into artificial pasture, the *Phormium* association of semi-swamp, successions following the felling of swamp-forest, *Hebe* shrubland, Induced fell-field and herb field on Mount Miromiro, an induced subalpine cushion-plant association on the Richardson Mountains.

(b) VARIOUS GRASS AND HERBACEOUS PLANT-COMMUNITIES.

(1) D A N T H O N I A   P I L O S A GRASSLAND.—This distinct association demands further treatment.   The fundamental fact is that a plant-formation, for such is low tussock-grassland, having the distinct ecological stamp of dominance by the tussock life-form, has been replaced by another plant-formation distinguished by the domination of a turf-forming grass, *Danthonia pilosa*, frequent burning coupled with continuous sheep-grazing being the main factor.* Although, at first glance, it would appear there was little else than this species in a typical pasture, this is far from being so.   Thus, a piece of lowland *danthonia* † grassland, as it occurs in the dry northern part of the North-eastern District, possesses a good many other species, indigenous and exotic, their presence and relative abundance depending upon that lack of uniformity in habitat present in all pastures, which is such a stumbling-block in ascertaining their composition and economic value.   The following is a list of some common species : (indigenous) *Cheilanthes Sieberi* (specially dry ground), *Agropyron scabrum* (in *Discaria* bushes, and so hardly eaten), *Acaena novae-zelandiae*, *Geranium sessiliflorum* (two distinct jordanons), *Discaria toumatou* (more or less prostrate, frequently eaten by rabbits), *Pimelea prostrata*, *Leucopogon Fraseri*, *Dichondra repens*, *Gnaphalium collinum* : (exotic) stunted *Dactylis glomerata*, *Holcus lanatus* (wettish places), *Anthoxanthum odoratum*, *Sanguisorba officinalis* (perhaps sown), *Trifolium dubium*, *Hypochaeris radicata*, and *Calotis lappulacea*.   Certainly many more species belong to this type of grassland, these differing more or less in different localities.   Where the sheep ' camp ' and manuring is extreme, *Danthonia pilosa* is absent and the species present are *Acaena novae-zelandiae*, *Dactylis glomerata*, luxuriant *Hordeum murinum*, *Erodium cicutarium*, and *Cnicus lanceolatus* ; *Marrubium vulgare*, the plant *par excellence* of ' sheep camping ground ' was absent in this particular pasture.

H. H. Allan (1927, p. 74) describes a low tussock-grassland community, where, though both *Danthonia pilosa* and *D. semiannularis* are very common, it seems improbable that in the rather wet climate (Mount Peel, Eastern District) the former will ever dominate.

Equally interesting, especially from the standpoint of exotics replacing indigenes, is the occurrence of another type of *Danthonia* grassland in many parts of North Island (but not restricted thereto), where *D. pilosa* has invaded and replaced artificial pasture of sown European grasses, *Trifolium repens* (which according to Wallace (1889, p. 29) ' is exterminating many native species '), and other pasture-plants, the seeds of the invader being brought into the community by sheep.   In fact, farmers wishing to introduce *D. pilosa* into their pastures frequently procure sheep for that purpose from ' danthonia country ', a cheap and effective method.

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* Sowing seeds of exotic grasses, &c., is occasionally practised.

† The agricultural name of *Danthonia pilosa* is danthonia, under which name its seed is sold.

(2) INDUCED LOW TUSSOCK-GRASSLAND.—Where montane *Nothofagus clif-fortioides* forest is burnt in the North-eastern and Eastern Districts the ground is frequently invaded by species from the adjacent *Festuca* tussock-grassland, various mat-plants forming an early succession and functioning as seed-beds. On such the seeds of *Festuca novae-zelandiae* readily germinate. When fully developed, induced tussock-grassland of this class is not to be distinguished from the formation in general. Should the induced community occupy a gully, that portion on a dry slope facing north may contian a good deal of *Pteridium*, while, on the shady side, the tussocks will be exceedingly close, provided they have not been regularly burned. In the South Island low tussock-grasslands there are now many wide areas originally forest, their origin only to be known from comparative studies. In other places, the status of the grassland is clearly revealed by the presence of an occasional tree or a fallen log. In the lowland belt exotics hostile to the incoming of grassland occur, e.g. broom, gorse, and sweet-briar, or in some soils the indigenous *Leptospermum Scoparium*. Gorse and broom, however, are powerless at above 600 m. altitude or less, according to latitude.

(3) MAT OR TURF PLANT-COMMUNITIES WHICH HAVE REPLACED LARGE OR SMALL AREAS OF MONTANE OR LOWER-SUBALPINE LOW TUSSOCK-GRASSLAND.— Before the exploitation of the upland *Festuca* (*F. novae-zelandiae*) tussock-grassland of South Island which commenced some eighty years ago, the fescue tussocks grew so closely that very little else could exist in their shade. But with the advent of sheep-farming this condition of affairs was quickly changed, for, in order to get palatable food for his flock, the runholder, year by year and at all seasons, set alight the inflammable tussocks.* As this went on the tussocks gradually decreased in size (Pl. 5. fig. 6), while many died. Thus, bare ground suitable for plant-invasion became increasingly abundant. In the virgin community, owing to erosion and natural death of tussocks there was always some open ground where light-demanding species could live, and for these also were available particularly dry stony ground and other stations which they could occupy. Such plants, many of them of the mat and turf-making form, having now plenty of ground for their occupation, have formed various minor communi-ties, which, taken together, in many localities dominate the tussock-grassland. Thus a type of vegetation, distinct from the tussock-type, has by degrees come into being, thanks to the direct and indirect action of the sheep-farmer, and the two opposite types grow either side by side or so mixed that a third type has also been established. In the most arid areas, however, a fourth type has originated, which may be named ' steppe ' or ' semi-desert ', and which, even if all stock were removed, probably can never again revert to its primitive condition, so greatly is it altered both as to composition and life-forms.

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* An old tussock contains a great deal of dead dry stems and leaves, and so is highly inflammable during dry weather. Tussocks of this kind die naturally, but this only leads to small patches of open ground, a result not comparable with the effect of wholesale destruction by fire.

The new communities now being considered grow either side by side with the modified tussock-grassland, or within it as larger or smaller 'islands'. In different localities to the east of the Divide of South Island, as one proceeds from north to south, the species forming the new mat and turf communities differ to some extent, such differences depending chiefly on latitudinal and altitudinal distribution, with varying average annual rainfall and number of rainy days. A northerly (dry, sunny) aspect favours the transformation from the one type to the other, but with a southerly (moister, shady) aspect something not very different from the virgin association may persist. This is most striking in semi-arid Central Otago, where there are frequently plenty of tussocks on the shady side, but almost bare ground on the sunny side. All this is well-known by the sheep-farmer and his expressive terms 'dark face' and 'sunny face' might quite well be adopted by plant-ecologists.

Using the terms 'mat-plants' and 'turf-plants' in a wide sense, the following are the most important species in the new communities—tussock-grassland no longer—throughout a good deal of the North-eastern and Eastern districts :—
Blechnum penna-marina, Muehlenbeckia axillaris, Acaena inermis, A. microphylla, A. Sanguisorbae var. *pilosa*, and hybrids between the three last (two or all three taking part), *Pimelea prostrata, Epilobium pedunculare* (in a wide sense), *Hydrocotyle novae-zelandiae* var. *montana, Leucopogon Fraseri, Coprosma Petriei, Wahlenbergia albomarginata, Helichrysum bellidioides, H. filicaule, Gnaphalium Traversii*, and *Raoulia subsericea*. The rosettes, flattened to the ground, of *Plantago spathulata, Senecio bellidioides*, and the exotic *Hypochaeris radicata* are a common feature ; small tussocks of *Poa Colensoi* are abundant in many parts, and link the community to tussock-grassland proper; *Gaultheria depressa* (perhaps not equivalent to the type) may be almost pure in wettish places, and in the South Otago District such ground is closely occupied by the grass-like liliaceous *Herpolirion novae-zelandiae*. In the upper montane belt, or in places at a lower altitude, the great mats of *Celmisia spectabilis* may occupy the ground in such astonishing abundance as to form a distinct community, and even *C. novae-zelandiae* and *Cyathodes Colensoi* may be striking features, all three occurring at a far lower altitude than is usual. Most of the species cited above would be pasture weeds, pure and simple, were it not that they serve as seed-beds (Pl. **5.** fig. 6) for the entry or increase of economic species of grasses, &c. : they also function economically in checking denudation. As already mentioned, about seventy-four species of exotics occur in low tussock-grassland as against 216 indigenes, but a large number of such exotics do not enter into competition with the latter, since they occupy sheep-tracks, stony ground, and bare places, and do not properly belong to the community.

The following case is of particular interest, as showing for how long a period indigenous species can hold their own under specially trying circumstances. At the base of the Malvern Hills, where these abut on the Canterbury Plain (Eastern District, alt. 360 m.), according to notes taken by L. Cockayne in December 1901, there was a field, originally low tussock-grassland, which had

been frequently burned and continuously grazed, and often overstocked for a period of at least forty-one years. The grazing must have attained to about a maximum pitch of severity, for not only sheep, but cattle and horses were depastured, so that far more plants were constantly eaten than if sheep only had been used.* The horses, too, would be fed on chaff from time to time, and this, together with proximity to the adjacent high road, would bring in the seeds of many exotic plants again and again. With such a fierce attack upon the indigenes, many species of hostile exotics established, and constant severe mixed grazing, it seemed unlikely that any of them would still hold their own. On the contrary, according to the notes, the following indigenous species still formed part of the plant-covering :—*Plantago spathulata* (' very abundant, leaves pressed close to the ground '), *Geranium sessiliflorum* (' rosette-plant, leaves strongly aromatic '), *Oreomyrrhis andicola*, in a wide sense (' easily reproduced from seed '), *Cotula dioica* var. *crenatifolia* (' leaves bitter, has stout creeping stems ') ; ' where mounds of drier ground occur the native plants are more numerous ', e.g. :—*Leucopogon Fraseri, Helichrysum filicaule, Epilobium Hectori, Carex breviculmis, Senecio bellidioides, Poa Colensoi, Plantago spathulata, Wahlenbergia albomarginata, Sceleranthus biflorus, Dichondra repens, Geranium sessiliflorum, Colobanthus Billardieri* ; ' at one time *Chrysobactron Hookeri* [var. *angustifolia*] must have been abundant and, even yet, there are very many scattered plants '. The notes do not record the exotics, but the following were certain to be present : *Lolium perenne, Anthoxanthum odoratum, Dactylis glomerata, Poa pratensis, Agrostis alba, Trifolium dubium, T. repens, Prunella vulgaris*, and *Hypochaeris radicata*.

(4) R A O U L I A G L A B R A SUCCESSION AFTER BURNING SUBALPINE SOUTHERN-BEECH FOREST.—The eastern face of the southern portion of the Humboldt Mountains (Fiord District), from its base (300 m. alt.) up to rather more than 1200 m. altitude, was originally covered with *Nothofagus* forest, but this was partially burned in 1887 up to a height of about 900 m., many large patches of trees escaping the fire. In 1895 there was a second fire which made a clean sweep of the first remnants, and destroyed more virgin forest to the north. Shortly afterwards seeds of pasture-plants were sown over a great deal of the burnt area, but a broad belt, bounded above by the standing forest and below by a line at about 600 m., was left unsown. In 1921 much of the sown area, especially the more or less continuously grazed drier slopes, was covered with artificial grassland, but the gullies, with much land in their vicinity, were occupied by a bracken association which intergraded with the artificial grassland ; this contained a good deal of *Coriaria sarmentosa* and, in places, the exotic *Hypericum Androsaemum*. An unexpected feature was that the grassland had in it no tussocks of either *Festuca novae-zelandiae* or *Poa caespitosa*. However, certain other indigenes were common, e.g. *Danthonia setifolia, Triodia*

. * Different species of grazing animals select different plants as food. Thus *Senecio Jacobaea* is eradicated by sheep, but increases under the grazing of cattle, as does also *Chrysanthemum Leucanthemum.*

Thomsoni, Poa pusilla, Acaena Sanguisorbae var. *pilosa, Lagenphora pumila, Raoulia glabra,* and *Helichrysum filicaule.* White clover (originally sown) was far from common.

The upper unsown portion, commencing at an altitude of rather less than 600 m.,was clad with an unexpected plant-covering which, viewed from a distance, gave a brownish tint to the hill-side. This was due to the extreme abundance of the moss-like mats of the indigenous *Raoulia glabra* growing into one another and forming low hummocks, the whole being a carpet some 15 cm. deep. This formed an ideal seed-bed, for growing on the *Raoulia* were a good many species, some coming from below and others from above, including the following :— (exotics) *Holcus lanatus, Festuca rubra* var. *fallax, Trifolium repens, Hypochaeris radicata* ; (indigenes) *Hypolepis millefolium, Lycopodium fastigiatum, Danthonia setifolia, Poa caespitosa* (absent below), *P. intermedia* (absent below), *Acaena Sanguisorbae* var. *sericeinitens,* the shrubby *Hebe buxifolia,* the semi-woody *Veronica Lyallii, Celmisia coriacea,* and *Cassinia Vauvilliersii.* Undoubtedly the *Raoulia* community is an early succession, and, if we may prophesy, will be replaced by grassland and colonies of shrubs, and possibly the latter may be the climax ; or, of course, forest may return.

(5) INDIGENOUS SPECIES HOLDING THEIR OWN IN WETTISH GROUND (CHATHAM ISLAND).—Lowland swamp in Chatham Island in its shallowest parts is converted by the trampling of cattle into ground which can be occupied by pasture-plants, exotic and indigenous, the latter well holding their own in competition with the aggressive *Poa pratensis.* The following was the composition of such pasture according to notes taken by L. Cockayne in the summer of 1901 :—*Poa pratensis, Juncus* (a small species), *Potentilla anserina* var. *anserinoides, Myriophyllum pedunculatum, Epilobium nerterioides, Lilaeopis* sp., *Pratia arenaria, Lagenphora pumila, Helichrysum filicaule,* and *Gnaphalium collinum.*

(6) INDIGENOUS SPECIES INVADING BOWLING-GREENS.—The bowling-green at Queenstown (South Otago District, alt. about 304 m.) would originally be made by sowing *Festuca rubra* var. *fallax.* By degrees the three following species have crept in, the seeds of the first two having been brought by water used for watering the green :—*Hydrocotyle americana,* small rosettes of *Plantago triandra,* and a species of *Acaena.*

The Greymouth green (North-western District) also contains more or less of the *Plantago,* but, in addition, the coastal *Cotula dioica* arrived in silt used for topdressing the grass. The latter species has proved so excellent for the green that, according to Dr. W. McKay, its turves are now regularly planted in the green. The bowling-green at Westport now also consists mainly of indigenes, and we fancy its composition will be similar to that of Greymouth.

(7) INDUCED FELL-FIELD AND ALLIED COMMUNITIES.—In certain localities where subalpine forest or shrubland has been burned, or cut down, combinations of grasses, herbaceous perennials, low evergreen shrubs, &c., with wind-borne or bird-borne seeds, have come from neighbouring communities and formed

an induced community which may or may not bear a close resemblance to one already in existence, or which may belong to another class far different from that which formerly occupied the ground. When the community is open, and the bare ground excessive, it comes into the class ' fell-field,' but when closed or the bare spaces are small, it ranks as ' herb-field '. Between these two formations there are many transitions.

(α) *Where the subalpine-scrub of Mount Egmont (Egmont-Wanganui District) has been cut down* there soon appears in certain places a new community consisting, in part, of species forming herb-field at a higher altitude. The most important members in one place examined were :—*Poa anceps, Danthonia setifolia*, a var. of *Acaena Sanguisorbae, Ourisia macrophylla, Pratia angulata, Celmisia glandulosa* var. *latifolia* (confined to Mount Egmont), and *Senecio latifolius*. Even, where exotic grasses have been sown in a paddock where horses graze, many herb-field species have gained a secure foothold, including, in addition to those cited above, *Helichrysum alpinum* and probably others.

On the other hand, destruction of the subalpine scrub may lead to the increase and spread of the locally-endemic *Hebe salicifolia* var. *egmontiana* *, one of its important constituents. Again, the felling of the lower subalpine forest of Egmont, which is dominated by *Weinmannia racemosa*, has led to the incoming of subalpine-scrub species at about 300 m. lower altitude than such naturally occur, e.g. the *Hebe* (as above) dominant, *Nothopanax Colensoi* (North Island var.), *Coprosma tenuifolia*, and *Olearia arborescens*.

(β) *Induced fell-field.*—At the present time the fell-field plant-formation of the drier mountains as a whole is more or less modified, a state of affairs due principally to the pernicious custom of sheep-musterers setting fire to the shrubs and tussocks, in order to signal their position to their fellow-musterers traversing the slopes above or below. This burning, aided by sheep-grazing, has led through subsequent erosion to an extension of bare ground and instability of the substratum, to the incoming of a few exotics (especially *Rumex Acetosella*), and an alteration in the relative abundance of the species, for some—e.g. *Dracophyllum uniflorum* and *Aciphylla Colensoi* burn readily. When fell-field occurs on any mountain at a lower level than usual, it very probably is indigenous-induced, though not to be distinguished from a primitive community. Proof of its status is frequently to be afforded by indications that forest originally occupied its site. Thus, on the eastern face of Mount Torlesse (Eastern District) there is induced fell-field of this character, which at the end of December 1901 was apparently identical in character to that of a higher altitude.

A specially interesting case is that of the induced fell-field of Jack's Pass, to which merely four lines are devoted in ' The Vegetation of New Zealand ', ed. 2, p. 4. Jack's Pass is a low saddle somewhat below 900 m. altitude, which

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* This may be identical with the var. *paludosa* (Ckn.) Ckn. & Allan, so common in lowland swamps of the Westland Subdistrict, but this matter will not be settled until certain garden experiments are concluded.

leads northwards into a great mountain complex from the Hanmer inter-montane basin. At one time, possibly about fifty years ago, but it may have been much less, the area under consideration was covered with *Nothofagus* forest. At the present time the vegetation is much the same as when it was ecologically studied by L. Cockayne more than thirty years ago. In place of the forest the plant-covering is a mixture of tall tussock-grassland (*Danthonia flavescens, D. Raoulii* var. *rubra*, and a great number of hybrids between them) and fell-field approaching herb-field. The latter is chiefly distinguished by the presence in quantity of low tussocks of *Festuca novae-zelandiae* and *Poa Colensoi*, various mat-forming species of *Celmisia* and their hybrids, the large erect rosettes of *C. coriacea*, many shrubs, some prostrate and spreading (*Podocarpus nivalis, Exocarpus Bidwillii*), and other much smaller, depressed, or erect, of which the ericaceous *Pentachondra pumila* is extremely abundant. At a low estimate there are 140 species and hybrid groups in the association, and yet nearly all have arrived since the destruction of the forest, and the vegetation, some of its members exotics, has developed in the presence of overstocking* and has been burnt again and again.

(c) INDUCED COMMUNITIES OF LIGNEOUS PLANTS AND FERNS RESULTING FROM THE REMOVAL OF FOREST AS A WHOLE OR SOME OF ITS MEMBERS.

(1) GENERAL.—When forest has been wholly or partially removed by man's action many different plant-communities have come into being, the estab-lishment of such having depended upon many circumstances of which the following are of particular importance :—(1) the class of forest, (2) its lati-tudinal and vertical position, (3) whether destroyed by axe or burning, (4) whether the destruction was total or partial, (5) the edaphic and climatic conditions of the habitat, (6) the presence or absence of grazing and browsing animals and, if present, their species and numbers, (7) the nature of the sur-rounding vegetation. Perhaps a few remarks on some of these heads may be of interest.

Thus, *Nothofagus* forest usually produces its like from the very commence-ment of the new growth, or early on in its development one or more species of the genus dominates. On the contrary, in regard to rain-forest proper, many successions leading to a climax arise, but such climaxes are not all alike. As for the method of destruction, burning, if fierce enough, may make a clean sweep, and should there be no trees, &c., left standing in the vicinity such will be wanting in the primary successions, e.g. *Nothofagus* forest cannot reproduce its like if no standing trees of that genus grow sufficiently close to the burnt area. In forest removed by axe and saw and not subsequently burned, a good deal of the undergrowth will remain, and on its nature the early successions

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* After shearing, as many as four thousand sheep may be grazed for a time on the small area.

depend, such being governed by the life-forms of the surviving species, their relative numbers, and the amount of bare ground and its nature. Generally, in milling forest, only the trees suitable for timber are removed and, in time, it may be impossible to tell whether such a regenerated forest is primitive or induced. The presence of browsing animals, especially the red deer, may destroy the primitive stamp of a forest, yet, to the uninitiated, it may look primitive enough. Again, a semi-bog forest may be drained, and so its composition and structure be greatly changed thereby. What follows we present with considerable diffidence, for the whole question regarding that which is popularly called ' second growth ' is badly understood and greatly in need of thorough investigation.

(2) THE A R I S T O T E L I A S E R R A T A (WINEBERRY) COMMUNITY.—A close growth (Pl. 6. fig. 7) of the small tree *Aristotelia serrata* is exceedingly common in the lowland belt of North Island and South Island, where forest has been felled or burned. On the new ground, exposed to the full sunlight, its seedlings appear in their thousands, though no seed-bearing trees are in the immediate neighbourhood ; indeed, the species is a very rare constituent of forest, being found only where light is abundant (by sides of fairly wide streams) and usually in limited numers. Apparently, the seeds must have been in the soil for a very long time, since it seems impossible that birds can have conveyed them to the spot in so short a time, or have deposited them on that particular piece of ground. As well as its great number of seedlings, the dominance of *A. serrata* depends upon its rapid growth more than that of any of the species associated with it, and, in this respect, it about equals *Leptospermum Scoparium*.

A community where *Aristotelia* is only one of various species combined together into incipient forest is not uncommon. Thus, on the Mamaku Plateau (Volcanic Plateau District) at about 600 m. altitude, where tawa (*Beilschmiedia tawa*) forest had been felled, a new and dense undergrowth had arisen, the young trees ranging from four to seven years of age ; the following was the combination :—*Wintera axillaris, Aristotelia serrata, Fuchsia excorticata* (very common in second growth* generally), *Schefflera digitata, Coprosma grandifolia, Alseuosmia macrophylla,* and, on the floor, *Asplenium bulbiferum, Histiopteris incisa, Astelia nervosa* var. *sylvestris,* and *Microlaena avenacea* (a forest-grass which quickly extends its area on abundant light being let into the forest). In that locality there is *Rubus fruticosus* (linneon) in abundance, but the still greater need of bright light for this species is usually a bar to its joining the community.

(3) THE B R A C H Y G L O T T I S R E P A N D A COMMUNITY.—In certain localities (e.g. near Wellington City) where the tall trees have been removed from semicoastal forest, the small spreading, much-branched tree *Brachyglottis repanda,* distinguished by its large, thin, more or less oblong leaves, milk-white tomentose

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* This frequently comes about through suckers being put forth from the burnt stump, the species being most difficult to kill by means of fire.

beneath, has increased to such an extent as to be now a special feature of the landscape. Growing in its company, but, some of them in smaller numbers than in the primitive community, are most of the small trees and undergrowth characteristic of the virgin forest. The following are common species :— *Cyathea dealbata, C. medullaris, Muehlenbeckia australis, M. complexa, Macropiper excelsum,* juvenile *Knightia excelsa, Dysoxylum spectabile, Melicope simplex, Pennantia corymbosa, Melicytus ramiflorus, Myrtus bullata,* species of lianoid *Metrosideros, Nothopanax arboreum,* juvenile *Pseudopanax crassifolium, Suttonia australis,* species of *Parsonsia, Solanum aviculare, Coprosma grandifolia, C. lucida, C. rhamnoides, C. areolata, Olearia rani.*

(4) NEW RIVER-BED VEGETATION OF THE UPPER OTIRA VALLEY (WESTERN DISTRICT).—Where the rain-forest proper had been felled about 1896, the new vegetation in 1910 was as follows. *Olearia ilicifolia* * dominated in many places, and was still a most striking feature. Where there was abundance of light there were many broad mats of the rather rare *Rubus parvus* (outskirts of forest, not within). The other species included *Libocedrus Bidwillii, Podocarpus totara, Phyllocladus alpinus, Pittosporum divaricatum* (in a wide sense), *Wintera colorata, Rubus schmidelioides* var. *coloratus, Aristotelia fruticosa* †, *Elaeocarpus Hookerianus, Myrtus pedunculata,* and *Pennantia corymbosa.*

(5) COMMUNITIES OF BOGGY GROUND.—In the North-western and Western Districts there is a rather remarkable bog association known to the settlers by the Maori name ' pakihi ', which owes its presence to an impervious layer of ' iron-pan ' in the gravelly substratum. Apparently no part of the association is virgin, except perhaps portions of the wide area (recently visited by G. Simpson and J. S. Thomson) through which passes the Cascade River in South Westland. Be this as it may, in many places in Westland after the forest is felled bog conditions rule, and under the influence of greatly increased light *Sphagnum* takes possession of the extremely wet peaty ground, and the area, by degrees, is occupied by a combination of various trees or shrubs dominated by *Leptospermum Scoparium,* while, in open places, there are many massive tussocks of the cyperaceous *Gahnia rigida.* When *Sphagnum* is abundant, a characteristic constituent of the new community is *Dacrydium Colensoi,* a podocarp by no means everywhere in the virgin forest, but occurring here and there as the chief member of a distinct subassociation. With it in the new community there is a good deal of *Phyllocladus alpinus, Podocarpus nivalis,* and *Suttonia divaricata,* which is a characteristic shrub. At an altitude of about 750 m., the saddle between Reefton and Big River (North-western District) was originally covered with low bog-forest of *Nothofagus cliffortioides* dominant, together with a large percentage of the small podocarps *Dacrydium biforme, D. intermedium,* and

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* This low tree or small shrub, though very common in the subalpine belt of New Zealand generally, is an important member of lowland river-terrace scrub of Westland, so its appearance in an early forest-succession is not as surprising as it might appear.

† When the same locality was visited recently, there was plenty of *Aristotelia serrata* and × *A. fruserrata.*

Phyllocladus alpinus. As undergrowth there were various kinds of montane and subalpine shrubs. Much of this forest which occupied the actual saddle has been felled and, in 1923, four distinct communities were to be observed on the new ground. These were dominated respectively by *Leptospermum Scoparium*, *Dracophyllum longifolium*, great patches of a long-stemmed, dark green, water-holding moss, 2·5 to 5 cm. deep, and low cushions of the wiry shrub, *Cyathodes empetrifolia*—which community is alone dealt with here. The open, soft, convex cushions of the *Cyathodes* are about 60 cm. across and 22 cm. deep, and in places so close together as to touch. Some other members of the community are *Gleichenia alpina*, *Holcus lanatus* (exotic), a form of *Danthonia semiannularis*, cushions of *Oreobolus pectinatus*, *Rumex Acetosella* (exotic), seedling *Leptospermum Scoparium* (eventually to change this early succession into shrubland), *Gaultheria depressa*, and *Hypochaeris radicata* (exotic).

(6) FERN COMMUNITIES COMING IN AFTER THE BURNING OF FOREST.—The case of bracken heath is too well known to need discussion here, and the incoming of *Paesia scaberula* and *Histiopteris incisa* after bush-burns has already received notice. *Hypolepis rugosula* and *H. punctata* also have their areas of occupation extended by the burning of forest. The great increase in the tree-fern colonies of *Dicksonia squarrosa*, owing to its stoloniferous habit, has been referred to already. In Chatham Island, that small, far-outlying, easterly part of the Region, it was noted (Cockayne, L., 1902, p. 311) that in one locality where the semi-coastal forest had been burned (a rare occurrence) a considerable area of land was almost entirely covered by a close community of tree-ferns. On the road-sides throughout the coastal plain of Westland, where the forest has been removed, there are many long stretches of *Gleichenia Cunninghamii* (Pl. 6. fig. 8) frequently associated with *Lycopodium volubile*. In any part of the two main islands where there is a forest climate artificial banks are quickly covered by the great leaves of *Blechnum procerum*, this fern increasing vegetatively so that a most striking physiognomic primeval plant-community is exactly reproduced. Recently made ditches are colonised early on by a small epharmone of the above-mentioned species. In one of the alluvial flood-plains of Westland, after a bush-burn of the swamp-forest, and establishment of an artificial pasture, the latter is now closely occupied by the great, much-branched mounds of the semi-tree-fern *Polystichum vestitum*, so that the area greatly resembles a swamp, where the niggerhead (*Carex secta*) is dominant. In this case, doubtless, the fern was not entirely destroyed by the fire, and its powerful branching habit led to its rapid reinstatement. So, too, this fern greatly increases its area of occupation where the trees have been cut down in subalpine forest. The miniature tree-fern *Blechnum Fraseri* behaves similarly when abundant light is let into kauri (*Agathis australis*) forest. Also when such forest has been destroyed and its site is being occupied by *Leptospermum Scoparium* one of the earliest species to enter the new community is *B. Fraseri*, which rapidly occupies much of the bare ground.

Sambucus nigra and *Cupressus macrocarpa* growing near indigenous forest are frequently invaded by the epiphytic ferns *Cyclophorus serpens* and *Polypodium diversifolium*, and extensive colonies are established on the rough bark.

(7) CHANGES IN PROGRESS IN THE FOREST REMNANT OF THE TOWN BELT, DUNEDIN.—This tree-community is a piece of the original forest of Dunedin, but, in course of time, many changes have taken place in its structure, &c., most to be traced to the influence of man. At the present time *Melicytus ramiflorus* is displacing *Fuchsia excorticata* (usually an aggressive species) over wide areas, and associated with it are *Nothopanax Colensoi* (South Island var.), *Pittosporum tenuifolium. P. eugenioides, Carpodetus serratus, Griselinia littoralis*, and *Hebe salicifolia* var. *communis* (not a true forest-species). *Aristotelia serrata* is less common than formerly, but far more so than it would be in the original forest.

(d) VEGETATION OF NEW GROUND.

(1) GENERAL.—In many cases such artificial sites as are caused by man's activities come much into the same category as that due to his agricultural and horticultural operations, and are eminently favourable for occupation by exotics. Waste ground in general road-sides, railway embankments, &c., are rapidly seized on by various free-seeding quick-growing annuals, and certain shrubs and herbaceous perennial plants also play a considerable part. Where the new ground is in Europeanised New Zealand, as is so frequent, and indigenous species are absent, then only exotic-induced communities, or weeds, can be expected. On the other hand, should indigenes be in close proximity to the new station, they may gain a footing and form part of a mixed community. This is frequent where a railway-line passes through modified or primitive communities. Example after example of this class could be cited, here only one or two of rather more than passing interest are mentioned.

Thus near the mouth of the tunnel near Waianakarua (North Otago District) on the sides of the Christchurch–Dunedin railway-line between the track and the fence, growing amongst various exotics, a few years ago there was an abundance of the striking *Celmisia Hookeri*. Near Raurimu (Volcanic Plateau District— altitude 585 m.) there grows on a railway-cutting a remarkable swarm of hybrid Gaultherias.

(2) VEGETATION OF GOLD-MINING TAILINGS.—Where there has been sluicing or dredging great heaps of stony debris are a common feature of the landscape in certain parts of New Zealand. Here only the vegetation of two different classes of tailings can be dealt with, both in the valley of the Taramakau (North-western and Western Districts), the account being compiled from notes generously taken for this paper by Dr. W. McKay of Greymouth. Obviously the substratum offered by tailings differs greatly in different places according to the size of stones, their petrological nature—schist, granite, greywacke, &c., the amount of silt and small stones present,—and its relation to light. Above all, however, the most important feature is the presence of grass in quantity, for upon this depends the degree of sheep-grazing to which the vegetation

is exposed. At Dilmanstown on an area of about 25 hectares, continuously grazed by sheep, there are these physiognomic features :—a close growth of the rosettes of *Blechnum discolor*, colonies of *Leptospermum ericoides*, but sometimes individual shrubs or trees of all sizes up to 3 m. high, deep breadths of *Paesia scaberula* (an early arrival), thickets of *Ulex europaeus*, but small plants are rare, and a mossy turf with mats of *Agrostis alba* (linneon) covering the banks of the mounds which form the irregular surface of the tailings. The principal remaining species of exotics are *Rumex Acetosella, Cerastium glomeratum, Rubus fruticosus* (linneon), *Hypericum Androsaemum, Digitalis purpurea* *, *Hypochaeris radicata*, and *Taraxacum officinale*. Indigenous species occur in greater numbers ; in addition the following are of importance :—*Dicksonia squarrosa* (frequently in groves), *Polystichum vestitum, Blechnum discolor, B. vulcanicum, B. procerum, B. penna-marina, Polypodium diversifolium, Lycopodium fastigiatum, L. scariosum, L. volubile, Arundo conspicua, Danthonia semiannularis, Carex comans* (exceedingly common as an indigenous-induced road-side plant in Westland), *Muehlenbeckia axillaris, Cardamine heterophylla, Weinmannia racemosa, Acaena Sanguisorbae* var. *pusilla* and probably other vars., *Aristotelia serrata, Myrtus pedunculata, Metrosideros hypericifolia* (as a mat), *M. perforata* (as a mat), *Leptospermum ericoides, Epilobium nummulari-folium, E. pedunculare* (in wide sense), *Gunnera albocarpa, Coprosma parviflora, C. rhamnoides, C. rugosa, C. brunnea, C. propinqua, Helichrysum bellidioides, Raoulia australis, R. tenuicaulis*, and *R. glabra*. Owing to the ever-present sheep-grazing, *Weinmannia racemosa*, a massive tree of forests, is to be seen only as a mat-plant, yet it occurs in such abundance that, were sheep removed, *Weinmannia* forest in time would occupy these man-made heaps of stone and silt and look as if virgin.

The vegetation of the Greenstone tailings of schist and granite, some four hectares in area, is probably about thirty years old. Grasses are absent and so no sheep modify the progress of events. This has led to the establishment of a different florula and vegetation from that just described. Thus, the only exotics of any moment are *Ulex europaeus*, but only in very small groups and an occasional plant here and there, and a good deal of a stunted form of *Hypochaeris radicata*. On the other hand, the following species of indigenous plants were noted :—*Polystichum vestitum, Blechnum penna-marina, B. discolor, B. vulcanicum, Pteridium esculentum, Lycopodium fastigiatum, L. scariosum, L. volubile, Libocedrus Bidwillii* (occasionally), *Podocarpus ferrugineus* (occasionally), *P. totara* (occasionally), *P. acutifolius* (occasionally), *Dacrydium cupressinum* (fairly common), *Arundo conspicua, Muehlenbeckia axillaris, Quintinia acutifolia* (common—abundant in Westland forests), *Weinmannia racemosa* (abundant, average height 1·2 m.), *Rubus schmidelioides* var. *coloratus* (scrambling on ground), *Pimelea prostrata* (common), *Metrosideros lucida* (common,

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* Where the climate is not too dry, the foxglove, after forest is burnt frequently, clothes the hill-sides as far as the eye can reach, but is eventually wiped out by bracken, unless pulled up in order to comply with the noxious weed regulations, in which case a good seed-bed is provided and the plant receives a new lease of life !

up to 1·2 m. high), *Leptospermum ericoides* (free seedlings up to 6 m. high), *Epilobium pedunculare* (fairly common), *Dracophyllum longifolium* (very rare), *D. Traversii* (very rare), *Suttonia divaricata* (common), *Coprosma parviflora* (this and the other species cited of the genus are fairly common), *C. propinqua, C. rhamnoides, C. rugosa, C. brunnea, Olearia ilicifolia, O. arborescens, O. avicenniaefolia* (only occasional).

The above list shows that forest-species predominate, so that Dr. McKay's notes declare that ' in 13 to 20 ' years forest will be established with *Weinmannia racemosa* and *Metrosideros lucida* dominant, and certainly *Quintinia acutifolia* will form a large proportion of the small tree and tall shrub undergrowth, but unless a number of other species, not listed above, come in, the new community will differ considerably from any of the Botanical District. Groves of *Leptospermum ericoides* are also a conspicuous feature of the new vegetation.

(3) Vegetation of cuttings (rock and clay banks).

(α) *In Wellington City.*—Once out of the actual business parts of most New Zealand cities there are frequently remnants of the original vegetation, so that many indigenous species are at hand ready to dispute the possession of the soil with the far more numerous exotics.   Generally speaking, on banks— loamy, clayey, or stony—exotics make pure, or almost pure, communities, *Dactylis glomerata* being particularly aggressive, as it is in similar positions everywhere ; yet even in such positions, particularly if shady, the indigenous *Poa anceps* frequently forms large sheets, greatly hostile to colonization by other plants.   Where the earth-cuttings have been made through a forest-remnant, various species may form a fringe round the upper margin of the cutting and extend more or less on to the bare ground, e.g. *Rubus australis, Metrosideros hypericifolia, M. perforata*, and *Polypodium diversifolium*.   In many places gorse and broom come on to the banks and make close thickets.   These two shrubs may also occupy considerable areas of steep rock (greywacke) cuttings. But, in such a station, a certain indigenous shrub is a formidable competitor for a permanent position on the rock, indeed, it may also forbid the incoming of gorse, broom, or cocksfoot on shady earth-cuttings.   This shrub is *Hebe salicifolia* var. *Atkinsonii*, which, according to circumstances, is much-branched and, in places, 2 m. high or more, or prostrate, semi-prostrate, and spreading. As soon as bare rock is ready for occupation by higher plants, thanks to lichens, bryophytes, and disintegration, seedlings of the *Hebe* are very soon in evidence.*

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* *Hebe salicifolia* is a large compound species for which six well-marked varieties (easily recognizable jordanons) have been or will shortly be described, and, in addition, there are many smaller virtually true-breeding groups (also jordanons), but far too close to one another to admit serviceable diagnosis.   Out of all this great collection of closely-related forms, the var. *Atkinsonii* is the only one which has this strongly-marked rupestral habit ; other forms may occasionally grow on rocks, but they do not ' select ' such a substratum. It appears probable that var. *Atkinsonii* is the type of the species.   If so, then one would almost be forced to place the remainder of the group together as another compound species under a new binomial name.

Amongst other indigenous plants which are frequently seen on Wellington rock-faces are *Cyclophorus serpens, Polystichum Richardi, Danthonia semi-annularis, Metrosideros perforata, Leptospermum Scoparium* (characteristic), *Epilobium nummularifolium, E. pubens, E. rotundifolium,* and *Brachyglottis repanda.*

(β) *In Dunedin City and neighbourhood.*—Wherever indigenous species are not far away many of them gain a place on rock-cuttings. The following are more or less common in such stations, but not all in any one place :—*Blechnum procerum, Asplenium flaccidum, Polypodium diversifolium, Pteridium esculentum, Leptospermum Scoparium, L. ericoides, Griselinia littoralis, Suttonia australis, Gaultheria rupestris, Cyathodes acerosa, Dracophyllum longifolium, Olearia avicenniaefolia, Raoulia glabra, Helichrysum glomeratum,* and *Cassinia fulvida.*

In deserted quarries the following species occur :—(exotic) *Pinus insignis, Dactylis glomerata, Cerastium glomeratum, Ulex europaeus, Cytisus scoparius, Hypochaeris radicata, Sonchus oleraceus* ; (indigenous) *Asplenium flaccidum, Polypodium diversifolium, Dichelachne crinita, Muehlenbeckia complexa, Griselinia littoralis, Fuchsia excorticata, Melicytus ramiflorus, Erechtites prenanthoides,* and *Gnaphalium luteo-album.*

IV. REPLACEMENT OF EXOTIC COMMUNITIES BY INDIGENOUS PLANTS OR THEIR INVASION BY SUCH.

Several examples of replacement of exotics by indigenes or their invasion by the latter have been dealt with already. Probably the most striking is the replacement of artificial pasture by one with *Danthonia pilosa* dominant. Here we call attention to certain interesting cases not previously recorded.

(1) INVASION OF ULEX EUROPAEUS BY THE SPECIES OF RAIN-FOREST PROPER.—To the visiting botanist, as mentioned in the general section of this paper, nothing in New Zealand is more astonishing than vast areas of hill-sides or long stretches of stony river-bed golden* with gorse or broom, the species pure or mixed together. To him the sight cannot fail to afford ample confirmation of the reputed supreme colonizing-power of the exotics. Even the New Zealander generally thinks, if he thinks at all on the matter, that, when such communities are growing where forest once reigned, such forest can never return. Such a belief is erroneous. Certainly, where gorse or broom has seized on tussock-grassland, or river-bed, as a dwelling-place, and no powerful indigenous plants are at hand to dispute their ownership, a long time will elapse before the communities they dominate will change. On the other hand, where forest has been felled and burned, and even if European pasture-plants have become established by sowing, should the thickets of gorse or broom be in the close vicinity of forest, many forest-plants, even in the presence of sheep

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* Both *Ulex europaeus* and *Cytisus scoparius* are far from being simple species, for both are extremely polymorphic as to colour, size, and shape of flowers, period of blooming, and life-forms—a matter pointed out by L. Cockayne nearly thirty years ago.

and cattle, readily gain a footing beneath the thickets and, in course of time, will cut off the strong light such require and an early stage of forest be established. For example, where gorse and broom have replaced semi-coastal forest (Ngaio, Wellington) under the conditions indicated above, young tree-ferns, trees, and shrubs are abundant beneath these exotics where the illumination is favourable, and the following species are common :—*Cyathea dealbata, Pteridium esculentum* (its lianoid epharmone), *Adiantum affine, Blechnum lanceolatum, Muehlenbeckia complexa* var. *trilobata, Pittosporum eugenioides, P. tenuifolium, Aristotelia serrata, Elaeocarpus dentatus, Myrtus bullata, Nothopanax arboreum, Suttonia australis, Geniostoma ligustrifolium, Parsonia heterophylla* (especially common), *Myoperum laetum, Coprosma robusta, C. rhamnoides, Olearia rani,* and *Brachyglottis repanda.* When such of the above, and others not cited, which are trees or tall shrubs, grow above the gorse or broom thickets, as the latter are strongly light-requiring, they die in a short time—a happening analogous to *Aristotelia serrata* or *Leptospermum Scoparium* being overpowered in an early forest succession.

(2) REPLACEMENT OF L E Y C E S T E R I A, H Y P E R I C U M A N D R O S A E M U M, AND C Y T I S U S S C O P A R I U S.—In several localities near Dunedin (Simpson and Thomson, 1928, p. 335), where after forest had been destroyed there had come a close community of the exotics, *Leycesteria formosa, Hypericum Androsaemum,* and *Cytisus scoparius,* this is now being replaced by various trees and shrubs. For instance, in one area the invading indigenes are the all-powerful *Leptospermum Scoparium* and *L. ericoides* ; in another area the invaders also include *Hebe salicifolia, Pittosporum tenuifolium, P. eugenioides,* and several species of *Coprosma* ; and in another area all the above are present together with *Suttonia australis.*

(3) A SERIES OF SUCCESSIONS ENDING IN COMPLETE DOMINANCE OF P H O R M I U M T E N A X.—A large part of the slopes of Flagstaff Hill—that picturesque mountain (666 m. alt.) dominating the city of Dunedin—is occupied by an astonishing mixture of exotic and indigenous plants, the latter in many places holding their own or even increasing. Many interesting cases pertinent to our subject could be cited, but we select one only, where, after many years' competition between the opposing exotics and indigenes, the latter are now the victors in the shape of thickets of *Phormium tenax,* that huge, all-powerful, somewhat *Iris*-like plant declared to be incapable of resisting the attack of the comparatively insignificant white-clover. At the present time, on a portion of the area under consideration, bracken is dominant, but it is gradually being replaced by *Phormium* (Pl. 7. fig. 9), so that a community of superlative powers of aggression, mixed rather than an indigenous-induced, is being replaced by another of a usually far less aggressive character (Pl. 7. fig. 10). The exotic species number more than fifteen, and amongst them are the following which are distantly aggressive :—*Dactylis glomerata, Agrostis alba* (linneon), *Poa pratensis, Holcus lanatus, Rumex Acetosella, Trifolium repens,*

Cirsium arvense, and *Hypochaeris radicata*. The indigenous species number more than twenty-five, apart from *Pteridium* and *Phormium*, and are mostly those common in rather moist tussock-grassland.

(4) ENTRY OF A SPECIES OF A REMARKABLE LIFE-FORM INTO A CLOSED STRONGLY GRAZED, INDUCED-MIXED COMMUNITY.—At one time there were extensive thickets of *Aciphylla Colensoi* in low tussock-grassland in general, but in that formation this species is now present only in greatly reduced numbers. This has arisen through the periodical burning* of the grassland, the plant being remarkably inflammable. Hares also feed on the rather succulent root. The species, and its allies, are tall plants of the *Yucca*-form with hard, stiff, bayonet-like, yellowish green, bipinnate leaves, and the plant itself is about 55 cm. high and 80 cm. diam. The seeds are so highly viable that in J. S. Thomson's garden the species is a horticultural weed, yet there are now wide areas of modi-fied low tussock-grassland where the plant no longer occurs. On Flagstaff Hill, Dunedin, there is a field with a close sward made up of various grasses, &c., which for many years has been constantly grazed by stock. For some time past the area has been invaded by *Aciphylla Colensoi* (Pl. 7. fig. 10) and the invasion still continues as evidenced by the presence of no few seedlings, so that the plant is now firmly established, notwithstanding the presence of the supposedly redoubtable white clover and *Hypochaeris radicata*, and the really antagonistic *Dactylis glomerata*. The community also affords another interesting example of the fact that the exotics and indigenes can flourish side by side even in the presence of continuous grazing, trampling, &c. The following is a list of most of the indigenous species present :—*Dichelachne crinita, Luzula* (one or more of the polymorphic ' *campestris* ' group), *Colobanthus crassifolius, Ranunculus multiscapus, Epilobium chloraefolium, Halorrhagis depressa, Hydro-cotyle novae-zelandiae, Gaultheria perplexa, Leucopogon Fraseri, Nertera setulosa, Celmisia longifolia, Helichrysum filicaule, H. bellidioides*, and *Gnaphalium Traversii*.

V. SUMMARY.

1. The paper deals, though far from fully, with the effect of settlement in New Zealand in regard to the primitive vegetation, and it may also be considered a supplement to Part III. of ' The Vegetation of New Zealand ', ed. 2.

2. Taken, as a whole, the paper is an explicit denial of the mischievous biological belief, even yet common, that in the ' struggle between the indigenous and exotic elements of the present flora the latter element is all-powerful.'

3. According to the most recent estimate, the flora of New Zealand consists of 1850 species, 427 groups of species-hybrids, a great many varietal hybrids, and 650 exotic species.

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* T. Kirk (1896, p. 19) considered that *Acipylla Colensoi* had been overcome by ' self-sown pasturage plants ' and that ' when once its vigour is reduced the ultimate destruction of the Spaniard [its popular name] is only a matter of time '.

4. In respect to the vegetation, the following terms used in the paper are defined :—primitive, modified, induced, and the last embraces indigenous-induced, exotic-induced, mixed, and artificial.

5. Competition between the indigenous and the exotic elements is far less severe than is usually considered, each element consisting mainly of different classes of life-forms, and each element for its greater part restricted to a different group of edaphic habitats, the indigenous to those of undisturbed soil, and the exotics to those of greatly disturbed soil.

6. Altitude also plays an important role, the exotics being essentially species of the lowland belt and decreasing both in numbers and power of attack with increase of altitude.

7. The struggle between indigene and exotic is very rarely an equal one, for the latter is generally greatly aided by the introduced grazing and browsing animals, nor must it be forgotten that such were wanting in primitive New Zealand.

8. The exotics have entered into no part of the primitive vegetation—rock and aquatic communities excepted.

9. Where the balance of nature in the primitive vegetation has been upset by the direct or indirect actions of man, a number of indigenous species have broken their bounds and become weeds equal in that undesirable status to any that have been introduced, *Pteridium esculentum* and *Leptospermum Scoparium* being indeed worse.

10. This matter of observing indigenes becoming weeds is of particular scientific interest, for the origin of the weed-host of Europe must surely be wrapped in obscurity.

11. Amongst forest-weeds an outstanding class is those which cut off a large part of light from the ground and inhibit, or make difficult, the establishment of seedlings which can develop into trees.

12. Tree-ferns and semi-tree-ferns belong to the above class, and it is shown how certain of these increase greatly by vegetative means, a fact hitherto unpublished.

13. In addition to indigenous-induced weeds there are many indigenous-induced communities, a number of which were unknown in primitive New Zealand, and a selection of such cases forms an important part of the paper.

14. Particularly interesting is the example where a forest, not greatly different from that of the neighbourhood, is being established on heaps of gravel, stones, and silt (gold-mining tailings) in competition with exotics.

15. A few cases are discussed of indigenous species entering into and eradicating powerful exotic-induced communities, e.g. that dominated by gorse and broom being invaded by rain-forest species, including tree-ferns.

16. Another unexpected example—but now quite commonplace—is artificial pasture of European grasses and clovers being transformed into one dominated

by an indigenous grass (*Danthonia pilosa*), such a community being unknown in primitive New Zealand where *D. pilosa* must have been not particularly common.

17. Still another example is the invasion of an induced-mixed, heavily-grazed pasture by *Aciphylla Colensoi*, once a highly-important member of montane low tussock-grassland, but now greatly reduced in numbers by fire.

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NEW ZEALAND PLANT-COMMUNITIES

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EXPLANATION OF THE PLATES

PLATE 3.

Fig. 1. *Dicksonia squarrosa* (a tree-fern), showing its method of vegetative increase. Photo Simpson and Thomson.

Fig. 2. A path cut through the rain-forest proper of South Westland bordered by *Dicksonia squarrosa*, showing the result of its vegetative reproduction, their close growth, and the powerful effect of groups of this fern in cutting off light from the ground. Photo Simpson and Thomson.

PLATE 4.

Fig. 3. *Blechnum discolor* (a semi-tree-fern), showing its method of vegetative increase. Photo Simpson and Thomson.

Fig. 4. A colony of *Blechnum discolor*, showing how it forbids almost any plant to become established beneath its shade. *Nothofagus* forest near Dunedin. Photo Simpson and Thomson.

PLATE 5.

Fig. 5. *Eucalyptus* plantation of the State Forest Service on the volcanic plateau (North Island) invaded by the indigenous small tree *Nothopanax arboreum*. Photo directed by L. Cockayne.

Fig. 6. Tussocks of *Festuca novae-zelandiae* established on stony debris, thanks to their seeds having fallen on an indigenous mat-plant. Montane low tussock-grassland area of Eastern District. Photo W. D. Reid (Dept. of Agric.).

PLATE 6.

Fig. 7. A first succession after destruction of rain-forest proper consisting of *Aristotelia serrata*. Near Dunedin (South Otago District). Photo Simpson and Thomson.

Fig. 8. Bank in South Westland from which rain-forest proper had been removed, now closely occupied by *Gleichenia Cunninghamii*. Photo Simpson and Thomson.

PLATE 7.

Fig. 9. A close growth of *Phormium tenax* replacing *Pteridium esculentum* and various indigenous and introduced plants. Flagstaff Hill, near Dunedin. Photo Simpson and Thomson.

Fig. 10. Invasion of a heavily-grazed field of indigenous-exotic (mixed) pasture, by *Aciphylla Colensoi*—an extremely common plant of primitive low tussock-grassland. Flagstaff Hill, near Dunedin. Photo Simpson and Thomson.

Burmese Charophyta. By B. P. PAL, M.Sc., University College, Rangoon.
(Communicated by Prof. F. E. FRITSCH, D.Sc., Ph.D., F.L.S.)

(PLATES 8-18, and 6 Text-figures)

[Read 22 January 1931]

THE present work is the outcome of a course of research at the Biological
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I. INTRODUCTION.

History.—Burmese Charophyta have received very little attention from
botanists, and though a few have been mentioned in Groves (1924), no serious
account of them has previously appeared. The present work deals mainly
with the systematics, the ecology—especially the influence of pH of habitat,
—and economic importance of the group. Original drawings have been given
for the new species and also for one of the old ones which was thought to be
particularly interesting. A full list of literature and synonymy is not included,
as this is already well provided in Groves and Bullock-Webster (1920).

Number of Species.—Charophytes do not attain their maximum distribution
in the Tropical Zone, being much more abundant in the temperate regions of the

world.   Burma, however, appears to be quite rich, and the number of species recorded is now not very much less than that for the whole of India.   In Groves, ' Indian Charophyta ' (1924), which may be taken as the standard work, thirty-six species are mentioned, of which two are unnamed, the material available not being sufficient for a proper determination ; a few more were added by Allen, making the number about forty.   During the course of the present work, in a period of scarcely a year, twenty-four species, nine of which are new, were collected and described, and these, together with five collected by others, make a total of twenty-nine species for Burma.   Incidentally, this serves to indicate a promising field for work for investigators in Burma.

The present work, however, was carried out under difficulties, most of which were occasioned by the short time available, and would have been overcome in due course, but the lack of literature was a particularly serious drawback.

In Burma, Charophytes are, together with a heterogeneous collection of aquatic plants, collectively dumped together under the term " ye-hnyi," and hence it is futile to enquire for them under that name.

Earliest Record.—The earliest recorded Charophyte for Burma appears to be *Chara brachypus* Braun, which was collected as long ago as 1890 at Sagaing in Upper Burma by Abdul Huk : this species has been collected by me after an interval of almost forty years, and the second record from Burma—a sterile plant of *Nitellopsis obtusa* Groves collected at Fort Stedman in Upper Burma in 1892, also by Abdul Huk.   During the subsequent years a number of species were added from time to time, but the localities given are not always exact, and sometimes are alluded to simply as " Burma."   Obviously, the value of a record is sensibly diminished when so vaguely indicated, for in a large province like Burma there are wide differences between the altitudes and climate of the different districts.

The exact nature of the habitat—still or running water, pond, lake, ditch, or drain—is always interesting, and may supply important ecological data. This requirement has been kept in view in the present work, and effort has been made to remove, as far as possible, all traces of ambiguity about localities.

II. TECHNIQUE AND METHODS.

Collecting.—Though a number of specimens were pressed for herbarium purposes, the majority of the plants were at once put into tubes or bottles usually containing formalin, as dried specimens do not give such satisfactory results for determination of species.   The pressed plants, however, withstood the drying well, and usually preserved their natural colour.

Fixing.—Charophytes, particularly the Nitellas, being extremely delicate plants, call for much care in fixing and staining in order to arrive at satisfactory results.   Most of the species were preserved in 2 per cent. formalin without special fixation, but these were much plasmolysed and rendered useless for cytological work.   The most satisfactory fixative used was hot alcohol, with which hardly any plasmolysis was noticeable.   The plants were plunged

into boiling 90 per cent. alcohol, and later preserved in the same fluid. A rather strong solution of chromo-acetic acid was also found to give a fair result.

Decalcification.—Many Charophytes are incrusted with lime, and it is often necessary to remove this in order to allow stains to penetrate and to see the details of cortex etc. A 5 per cent. solution of nitric acid, followed by washing in water, was found to achieve the desired result.

Staining.—Glycerine preparations were made in many cases, particularly during the monsoon months, when it was difficult to keep the absolute alcohol and the material from absorbing moisture from the humid atmosphere. The number of stains that can be used with glycerine are more limited than those available for the balsam method. Safranin and gentian violet stained well, but began to wash out in glycerine. The most useful stains were :—

Alum Carmine.—It was found that material could be left in this overnight without fear of overstaining, and it proved a good general stain.

Heidenhain's Iron Hæmatoxylin.—This was found to be excellent for observing the nuclei and was on the whole the most useful stain ; details of development in the species studied were mainly observed with the aid of this reagent. The schedule given in Chamberlain's 'Methods in Plant Histology' was followed, with the modification that the time in hæmatoxylin was much reduced.

Magdala Red.—A solution of this in 90 per cent. alcohol was found to give a pleasing brilliant stain.

With the balsam preparations a greater variety of stains were available. The alum carmine, magdala red, and iron hæmatoxylin were again successfully tried and gentian violet and safranin were used with fair results.

Microtomy.—For microtomy, the Cambridge Instrument Co.'s rocking microtome was used and sections 12 μ thick were cut. Sometimes it was found desirable to stain the material before embedding, as the decolorised pieces were difficult to locate in the molten wax or difficult to orientate when making the block. It was found difficult to infiltrate the mature oogonia as the thickening wall resisted the entry of the paraffin.

III. DISTRIBUTION.

A preliminary account of the distribution, both geographical and seasonal, has been given (Pal, 1929). Subsequently six more species were added, and alterations have had to be made in the seasonal distribution. The chief centres in and around which collections were made are :—

1. Rangoon, which may be taken as representative of the conditions obtaining in the large Delta area of Burma.

2. Mandalay, which may be taken as representative of the Dry Zone of Burma.

3. Toungoo, which may be taken as representative of the Intermediate Zone between the first two.

4. Maymyo and Taunggyi, which may be taken as representative of the large Shan Plateau.

5. Mergui in the extreme south of Burma.

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Some idea of the climatic conditions at the first four places may be obtained from the following table based on figures from various sources :—

	Rainfall. Approx. normal total for a year.	Temperature.		Altitude.	Zone.
		Average Temperature for January.	Average Temperature for July.		
Rangoon	100	76	81	Below 1000 ft.	Wet.
Mandalay	33	70	87	Below 1000 ft.	Dry.
Toungoo	84	71	81	Below 1000 ft.	Intermediate.
Maymyo	60	55	71	Above 3000 ft.	Shan Plateau.

Burma is profoundly affected by the monsoon, which usually lasts from June to September or even longer. The prevailing rain-bearing winds come from the south-west over the Bay of Bengal, and by reason of the position of the mountain ranges, the country is divided into two main regions, the Wet Zone and the Dry Zone, of which Rangoon and Mandalay may be taken as respective types. The two most important factors determining the vegetation are rainfall and elevation, though the edaphic factor is also of great significance.

The total number of species collected (not including species collected previous to this investigation and recorded by Groves (1924)), together with the localities wherein they were collected, are given in the following table :—

Name of Species.	Locality.
1. *Nitella acuminata*	Rangoon (Prome Road Ponds), Okkyin, Mingaladon.
2. *N. superba*	Maymyo, Taunggyi, Kyaikmaraw (near Moulmein).
3. *N. globulifera*	Maymyo.
4. *N. mucronata*	Rangoon (Prome Road Ponds), Mingaladon, Toungoo.
5. *N. batrachosperma*	Maymyo.
6. *N. elegans*	Maymyo.
7. *N. dictyosperma*	Toungoo.
8. *N. oligospira*	Rangoon (Prome Road, 8th mile).
9. *N. microglochin*	Mergui.
10. *N. burmanica*	Kyaikmaraw (near Moulmein).
11. *N. polycarpa*	Toungoo.
12. *N. furcata*	Rangoon (Victoria Lakes), Kamayut, Okkyin, and Nyaung-bin-zaik (near Moulmein).
1. *Chara Wallichii*	Toungoo.
2. *C. corallina*	Hsipaw (Northern Shan States).
3. *C. nuda*	Maymyo.
4. *C. hydropitys*	Toungoo, Mandalay.
5. *C. erythrogyna*	Rangoon (Victoria Lakes), Maymyo.
6. *C. burmanica*	Maymyo.
7. *C. flaccida*	Rangoon (Prome Road Ponds).
8. *C. gymnopitys*	Rangoon (Prome Road Ponds), Mandalay (moat and paddy fields), Maymyo, Taunggyi, Mingaladon, and Okkyin.
9. *C. Grovesii*	Maymyo.
10. *C. Handae*	Maymyo.
11. *C. brachypus*	Maymyo, Taunggyi.
12. *C. zeylanica*	Between Heho and Taunggyi, Mandalay (moat).

It should be mentioned that while only a few of the Charas are restricted entirely to mountainous areas (e.g., *C. nuda*, *C. Grovesii*) or to plain country (e.g., *C. Wallichii*, *C. hydropitys*), the Nitellas differ in that only one species (*N. superba*) has been found both in the hills and the plains ; even in this case there was much difference between the two forms. It would be premature, however, to attempt to draw any conclusion from this peculiar distribution of the Chareæ and the Nitelleæ until a much more complete record of their distribution is available. The Nitellas from the Maymyo Hills are particularly interesting, three of the four records being new species, and the fourth (*N. batrachosperma*) with the exception of two records by Allen from Gonda and Saharanpur, being unknown from India. Both as regards quantity and number of species the Charophyte flora from the hills is distinctly richer than that from the plains, and Maymyo yielded a better 'haul' than any place on the plains. Other species not previously recorded from Burma are *N. acuminata*, *N. dictyosperma*, *C. Wallichii*, *C. erythrogyna*, *C. flaccida*, and *C. hydropitys*. The new records of species previously known from Burma represent interesting extensions of distribution, since the localities noted are often hundreds of miles away from those previously mentioned.

Charophytes were found to flourish best between the months of August and March, dying out in the extreme dry season, and not reappearing till after the first month or so of the monsoon. Many species appear to flourish only within certain short periods, though a few are found throughout the greater part of the season favourable for growth. The following table gives an approximate idea of the seasonal distribution :—

Name of species.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March.
Nitella acuminata				......	......	......	......	......
N. superba				....				
N. globulifera		......	......	......	......			
N. mucronata			......	......	......	......	......	..
N. batrachosperma			......	......	......	......		
N. elegans	......	......	......	......				
N. dictyosperma						....		
N. oligospira					......	......	......	......
N. microglochin			....					
N. burmanica			......	......	......	......		
N. polycarpa				......	......	......	......	
N. furcata				......	......	......	......	
Chara Wallichii					....			
C. corallina			......	......	......			
C. nuda			......	......	......			
C. hydropitys		....	....					
C. erythrogyna	......	......	......	......	......	......	......	......
C. burmanica			......	......	......			
C. flaccida						...		
C. gymnopitys			......	......	......	......	......	......
C. Grovesii			......	......	......			
C. Handae			......	......	...			
C. brachypus		......	......	......				
C. zeylanica		......	......	......				

Though the distribution of most agrees with the table for Indian species given by Allen (1925), there are important differences, the most striking being the long-continued growth and much later occurrence of *N. acuminata*, the earlier appearance of *N. batrachosperma*, the much longer period of growth of *C. gymnopitys*, and the shorter period of *C. brachypus*. These periods must, however, be regarded as approximate, as there is liable to be much variation, while allowance must also be made for the capricious periodicity displayed by many species : a species occurring one year may, for no apparent reason, be completely absent from the same locality the following year. Thus large masses of *N. furcata* were noticed in a pond at Kamayut in December 1927, where the following year it was completely absent.

IV. ECOLOGY.

Observations on the changing vegetation of ponds and lakes.—When ponds and lakes in Rangoon and its vicinity were visited brief notes on the prominent features of the aquatic flora were recorded. The following general conclusions were reached :—

1. At the beginning of the rainy season and throughout the preceding hot dry season, the aquatic vegetation is usually poor in the number of forms, though those flourishing attain quite a large distribution. Filamentous algæ are scarce, as a rule, and it is the non-cellular and colonial forms, particularly of the Cyanophyceæ, that are then most conspicuous. *Clathrocystis aeruginosa* (Kütz.) is often present in such large numbers as to give a decided dark green tinge to the water. No Charophytes are to be met with at this time.

2. Soon after the onset of the monsoons, at about the middle of June, species of *Spirogyra* (probably *S. decimina* (Müll.) Kütz. and *S. turfosa* Gay recorded by Handa (1927) from Rangoon) make their appearance, and *Oedogonium* is plentiful, while by August *Chaetophora elegans* (Roth) Agardh is also common.

Salvinia is often present, while *Marsilia* is found practically all the year round, and *Eichhornia crassipes* retains a firm hold of any pond into which it is by chance introduced. During the first part of the monsoons *Trapa bispinosa* and *Nymphaea* sp. are prominent, and later on, in September, *Hydrilla* and *Utricularia*.

3. In Rangoon, Charophytes do not seem to make an appearance before the end of October. After that they are fairly common. In November *Chaetophora incrassata* (Hudson) Hazen is very common and *Batrachospermum* may very occasionally be met with.

4. During December and January many of the algal forms begin to produce spores and several forms, including species of Charophytes, to die out. The filamentous algal flora gradually diminishes till eventually the condition to be found during the dry and the first part of the rainy season is attained. This gradual decline is perhaps to be correlated partly with the drying up of the smaller ponds which are often richest in aquatic plants and partly to the increasing temperature, the optimum temperature for the plants being exceeded.

Relation of Charophytes to other aquatic vegetation.—Charophytes are seldom solitary in growth, being usually found in dense masses to the exclusion of other plants. An exceptional case was *C. hydropitys*, found in small clumps separated by masses of *Utricularia* etc. in roadside ponds at Toungoo. A community may be formed of one species only, e.g., *C. Wallichii* which was found growing in a small pond at Toungoo and *N. oligospira* which was found in large masses in Prome Road pools. Often, however, several species occur together, for instance, *C. burmanica*, *C. Grovesii*, *C. Handae*, and *C. brachypus* were usually found together in shallow drains at Maymyo, and *N. superba* and *C. Grovesii* were another common combination.

When conditions are favourable they may oust other plants in a pond, e.g., the *C. Wallichii* at Toungoo, obtained complete possession of a pond which a little earlier possessed a rich vegetation of reeds, *Nymphaea*, *Salvinia*, etc. It may, however, be ousted in turn by the invasion of more vigorous types, e.g., *Eichhornia crassipes*. *C. gymnopitys* forms a veritable carpet in some of the paddy-fields at Mandalay, while at Maymyo, what may be aptly described as ' forests ' of *Chara* and *Nitella* were numerous.

Ecological Factors.

Water.—The importance of water is, of course, fundamental, death ensuing from lack of it. It appears to be also one of the factors responsible for the decline of aquatic vegetation noticeable in the summer months, as the smaller ponds, which are often richest in vegetation, dry up. Apart from this it was observed that drying-up conditions appeared to favour and hasten the development of sexual organs. This was especially apparent in *N. acuminata*, discovered in a series of little pools at short distances from each other, alongside the Prome Road, Rangoon. The pools were of variable depth, some being almost dried up with not more than six inches of water, while others were from three to six feet deep. It was found that the plants in the latter either bore no game-tangia or, if gametangia were present, these were in very young stages of development, while the plants in the former were laden with sex-organs, and were profusely producing oospores. The rapidly diminishing supply of water was evidently the factor responsible for this marked difference. Amongst some algae, likewise, a favourable influence of drought on sexual reproduction has been noticed, notably in *Vaucheria* by Klebs (1896). The other ecological factors must be considered from the point of view of the aquatic habitat. They are :—

Light in water.—Light for photosynthesis is as important to the submerged water-plant as to the land-plant. Light in water is weakened, partly by reflection, partly by absorption, and partly by floating particles. Hence the dirtier the water the less the amount of light available, and light is a very important factor as far as Charophytes are concerned. Usually they grow in shallow water ; this is most commonly the case in Burma, though it is possible that in the larger lakes, such as the Inle Lake in the Shan States,

they may occur at greater depths. The degree of clearness of the water evidently influences this distribution, and in the clear water of Swiss Lakes they have been recorded from depths up to thirty metres.

Plants of *N. acuminata*, *N. oligospira*, and *C. gymnopitys* grown in glass jars and placed at a well-lighted window still suffered from lack of sufficient illumination, which was manifested by thin and lanky growth. Measurements of *N. oligospira* revealed the fact that the stem had decreased in thickness from 480 μ to 385 μ, and the length of the internodes had increased from one to three times the length of the branchlets to three to five times. Charophytes seem to flourish best in plenty of light which appears to be often a limiting factor in their distribution. Other water-plants, particularly the species with broad floating leaves, are often deleterious to their growth by reason of their shutting out some of the light. In this connection an interesting observation was made at Toungoo, where *C. Wallichii* was growing profusely in a small pond, filling up the greater area, during the latter part of November and the whole of December, at the end of which month the pond dried up. In October, however, when the same pond was visited, careful search revealed no trace of the plant, probably due to the fact that the floating leaves of *Nymphaea* sp. formed an almost continuous covering to the surface of the pond, which effectually prevented the light from reaching the depths. When the rapid fall of water in November caused the death of these plants, the *Chara* sprang into existence and obtained possession of the entire pond, so that by December no plant could be seen except the masses of sparkling, translucent green *Chara* dotted with thousands of minute orange-coloured dots representing the conspicuous clustered gametangia of the species. The dense growth of algal epiphytes, particularly species of *Oedogonium*, which often coats the stem and branchlets of Charas is probably also injurious, since it sometimes prevents the light from reaching a considerable area of the plant-surface.

Air in water.—Though the gases present in water are the same as those in the atmosphere, the properties are different, and air in water contains more oxygen and much more carbon dioxide in proportion to nitrogen than does the atmosphere. Air, however, reaches submerged parts with greater difficulty than the parts of plants growing in the atmosphere or in ordinary soil, and stagnant water is often poor in oxygen. It is probably to make the best use of the air dissolved in water, by presenting as large a surface as possible to the water, that the Charophytes are divided into so many segments. Probably for the same reason a few of the species have adapted themselves to grow in running water.

Temperature of water.—Though, being submerged plants, Charophyta are exposed to far less extremes of temperature than land-plants, some species are apparently extremely hardy with respect to their ability to withstand extreme temperatures. Thus *C. fragilis* is found in ice-water in northern regions and also in hot-springs at Yellowstone. This, however, does not apply

to all, and Warming's remark (1925) that 'the disappearance of many algae in summer may be due to their optimum temperature being exceeded' probably is true of many.

Substances dissolved in water.—Charophytes have the property of taking from the water in which they grow the calcium which is later deposited in the form of a calcareous incrustation, either irregular or made up of regular annular rings. Most species are limited to fresh water, but a few can accommodate themselves to the presence of salt, and grow in brackish water or even in the sea, e.g., *C. baltica*, which has been found in the Baltic Sea.

Hydrogen-Ion concentration of water.—As far as is known to the author, the action of this factor in relation to Charophytes has not previously been investigated, hence in the present work it has received much attention. The calorimetric method was adopted for the determination of pH values, as it does not require bulky or complicated apparatus. The indicators used were phenol red with a range of pH from 6·8–8·4, and thymol blue with a range from 8·0–9·6. The 9·6 value was attained once, while the lowest value was 6·9. The work was begun in August 1928, and determinations were made weekly, with the exception of a break in October, when the writer was absent on a collecting-tour, and when the pH of ponds containing Charophyta in Mandalay, Maymyo, and Toungoo were noted. The pH variation of the following five ponds and lakes all in Rangoon, was studied :—

1. *The Royal Lakes.*—A large, artificial, deeply indented lake, with a circumference of approximately three miles, immediately north of the town, with cultivated banks, used for washing clothes, bathing, boating, and various other purposes ; though an abundant aquatic flora is present, no Charophytes were discovered.

2. *Ponds in the Cantonment Gardens.*—A series of shallow inter-connected ponds at the foot of the Shwedagon Pagoda to the north of the town : here also no Charophytes were collected, though colonial and filamentous algae were fairly common.

3. *Godwin Road Ponds.*—A pair of shallow ponds with regular banks one on either side of the Godwin Road, connected with each other and with the ponds in the Cantonment Gardens mentioned above. The pH values were similar, the greatest difference being that of 0·3 on one occasion ; usually the difference was never more than 0·1. *Nitella acuminata* was collected from this pond.

4. *Victoria Lakes.*—A large stretch of deep water with indented wooded banks, largely used for bathing and boating, about four miles away from the town. The pH values may vary in different parts due to the large size of the lake, but the readings given below were all taken from samples of water collected near the Rangoon University Boat Club, where *Nitella furcata* and *Chara erythrogyna* were discovered.

5. *Kamayut.*—A small artificial pond which dries up in the hot season, but is particularly rich in vegetation, and yielded *N. furcata*.

The following table gives the variation in pH in the five ponds and lakes, with brief remarks on the Charophytes found in them :—

Date.	Royal Lakes.	Ponds in Cantonment Gardens.	Godwin Road Ponds.	Victoria Lakes.	Kamayut Pond.	Specimen found.
21– 8–28	7·7	7·6	7·6	7·6	6·9	Nil.
28– 8–28	7·6	7·7	7·6	7·6	7·0	Nil.
4– 9–28	7·7	7·6	7·6	7·6	7·0	Nil.
11– 9–28	7·7	7·6	7·7	7·5	7·3	Nil.
18– 9–28	7·8	7·6	7·7	7·6	7·3	Nil.
25– 9–28	7·6	7·3	7·6	7·1	7·4	Nil.
3–11–28	9·3	9·3	9·2	8·8	9·2	Young plants of *Nitella furcata* in Kamayut Pond and Victoria Lakes.
10–11–28	9·3	9·3	9·2	9·1	9·2	Do. Quantity increased 25 per cent.
17–11–28	9·4	9·4	9·4	9·3	9·3	Do. 100 per cent.
24–11–28	9·4	9·3	9·3	9·4	9·4	Do. 400 per cent.
1–12–28	9·5	9·4	9·3	9·2	9·4	Do.
8–12–28	9·5	9·6	9·4	9·4	9·5	Quantity diminished to 200 per cent. of original. *N. acuminata* in Godwin Road Ponds.
15–12–28	9·6	9·5	9·3	9·4	9·2	Quantity falls to 100 per cent.
22–12–23	9·3	9·5	9·3	9·2	9·2	Do. 25 per cent.
3– 1–29	8·8	8·6	8·6	8·8	8·8	*N. furcata* not found.
10– 1–29	8·5	8·4	8·3	8·4	8·2	*N. acuminata* flourishing.
17– 1–29	8·5	8·6	8·6	8·5	8·4	Do.
24– 1–29	8·7	8·6	8·6	8·6	8·7	Do.
31– 1–29	8·4	8·2	8·6	8·4	8·4	Do.

Toungoo.

Date.	Stream near Rifle Range.	Small Pond.	Marshy Water.
6–10–28	9·2	9·4	9·6
13–10–28	9·2	9·4	9·4
20–10–28	9·1	9·2	9·2
27–10–28	9·0	9·1	9·1

Readings at Maymyo and Mandalay during the third week of October were 8·9 and 8·8 respectively, and at Nyaungbinzaik and Kyaikmaraw, 9·3 and 9·5 respectively.

A consideration of the above table reveals the fact that the ponds in Rangoon have a pH range between 6·9 and 7·8 up to the end of September, after which there is a sharp rise to above 9. The following graphs (text-figs. 1–5) show this very clearly, and also the fact that there is not much difference between

TEXT-FIG. 1.
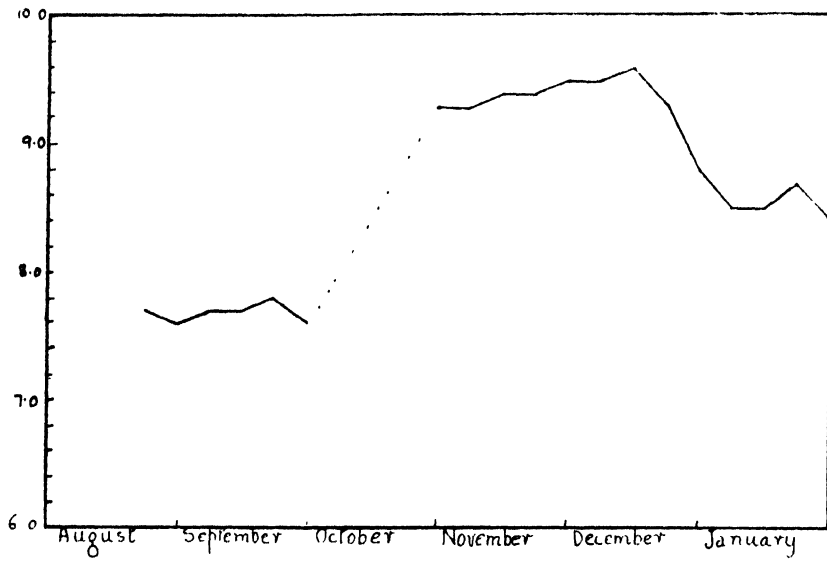
pH time-graph for the Royal Lakes.

TEXT-FIG. 2.
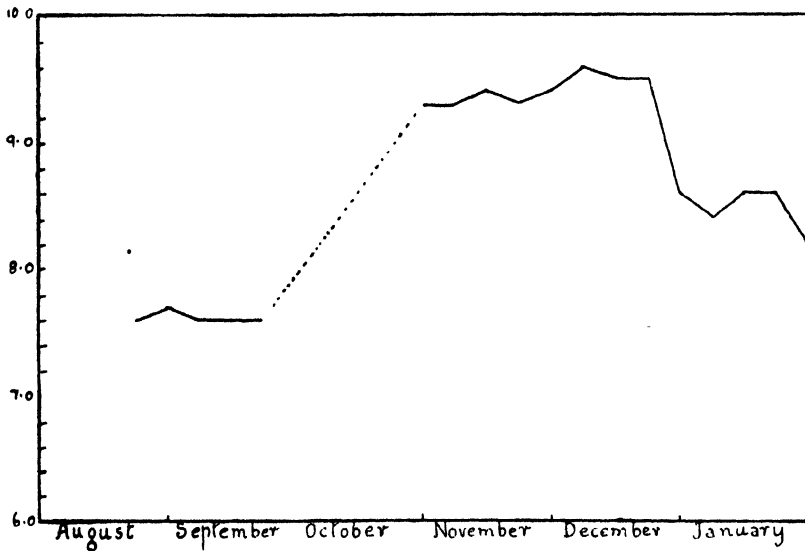
pH time-graph for Ponds in Cantonment Gardens.

TEXT-FIG. 3.

pH time-graph for Godwin Road Ponds.

TEXT-FIG. 4.

pH time-graph for the Victoria Lakes.
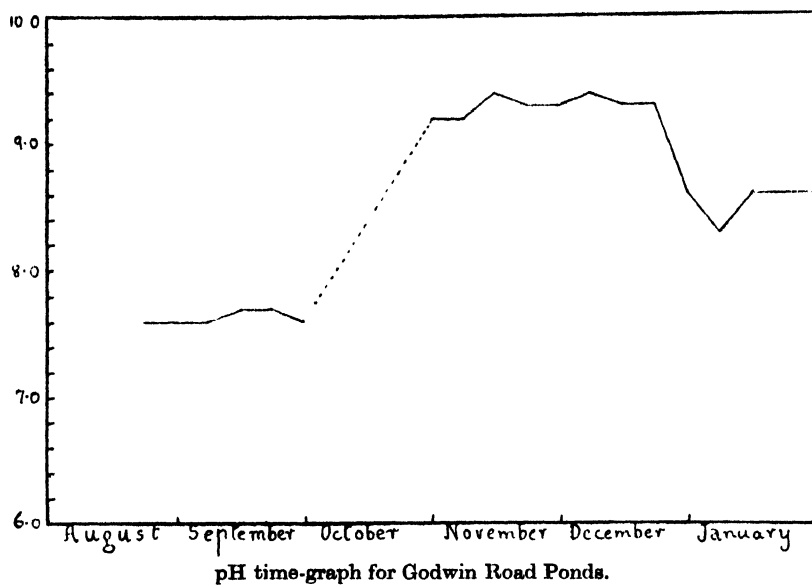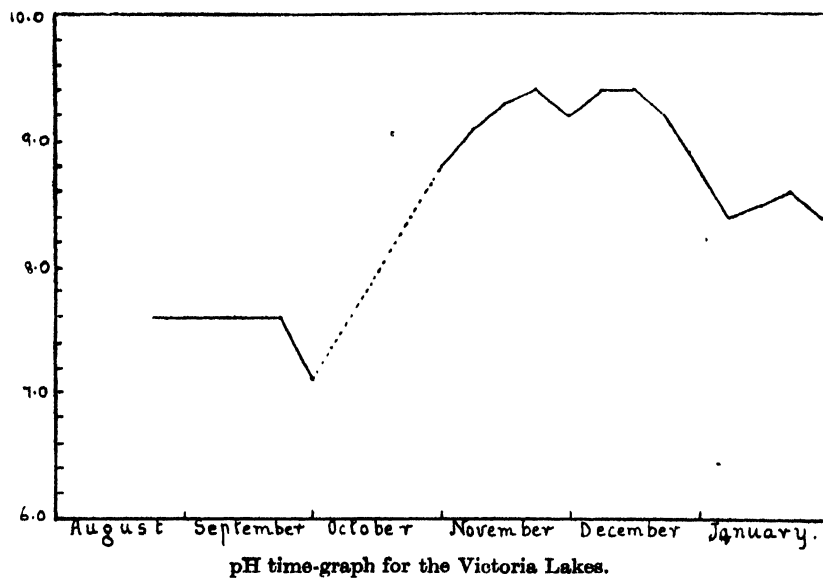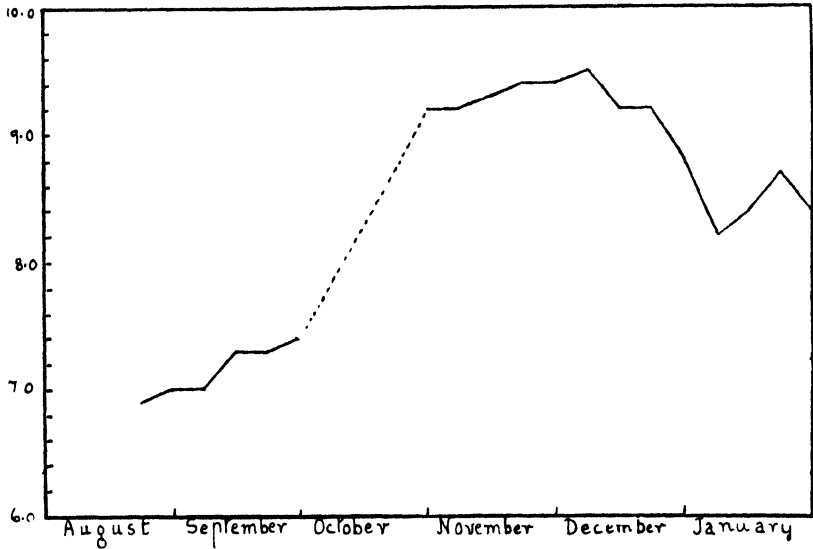
TEXT-FIG. 5.

pH time-graph for Kamayut Pond.

TEXT-FIG. 6.
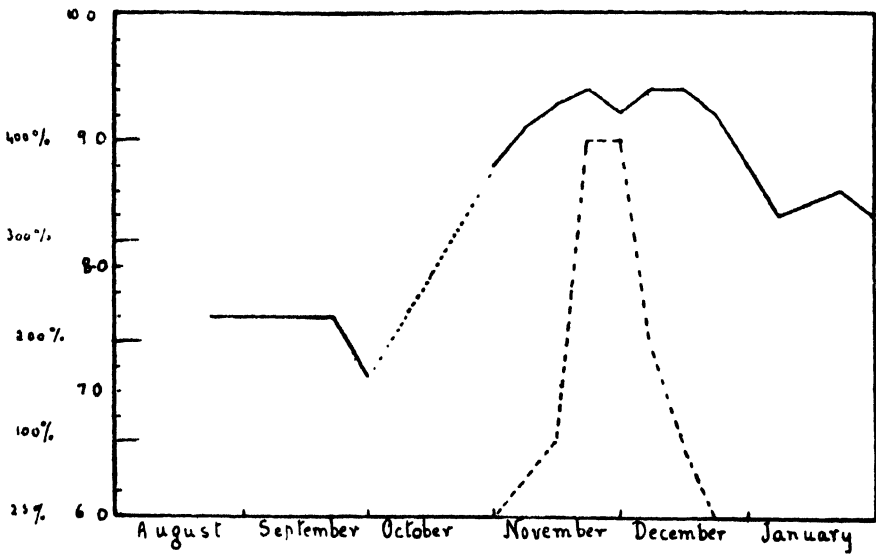
—— = pH variation in Victoria Lakes.
. . . . = Variation in quantity of *N. furcata* in Victoria Lakes (measured
in terms of percentage of quantity first discovered).

the pH variations of the several ponds. This is followed by a drop, though mostly there is again a small rise in the middle of January, and the highest values are attained at the end of November and the first half of December.

It is worthy of note that in Rangoon and its vicinity no Charophyte was discovered up to the end of September, i.e., while the pH range was between 6·9 and 7·8, though careful search was made. When, however, after that time the pH value rose to above 9·2, a fair number of Charophytes was obtained, and as most of these were young specimens it appeared that the growth had commenced only after the change of pH to higher values had occurred. As to what is responsible for the sudden rise in pH it is difficult to say, but it is evidently not the growth of Charophytes themselves, as high pH values were obtained in ponds which had no Charophytes in them.

In every case, however, when Charophytes were collected, it was from water with high pH values, and this was true not only at Rangoon, but also at Mandalay, Maymyo, Toungoo, and other places. From this it appears that there is some correlation between the growth of Charophytes and the pH value of the habitat, and that a high pH is favourable to their growth, while a low pH exercises an inhibiting influence. The graph obtained by plotting the pH values for Victoria Lakes and the increase in growth of *Nitella furcata* measured in terms of the percentage of the original quantity found against the time of the year shows that the maximum growth of the species is attained at nearly the same time as the highest pH values reached (text-fig. 6).

It must not be concluded, however, that there is a proportional relation between the value of the pH and the growth of the plant, for this is negatived by the appearance and disappearance of different species at different times, while the pH remains much the same. It appears safe to conclude, however, that growth is only possible in water possessing a pH range above a certain value, which appears to be about 8·0 for Rangoon species, and the maximum growth occurs at the time of the highest pH values. It would not be safe to apply this generalisation to all species till more work, and in other places, is done. It is interesting to note that Olsen's field-investigations and experiments (1923) suggest that hydrogen-ion concentration of the soil largely determines the composition of its plant-covering, and that, on the whole, there appears to be a fair correlation between the pH value of the soil and the vegetation it bears, and the average density of species per unit area increases as the pH value of the soil increases up to a certain point. The conclusion that the pH value of the water influences the growth of this group of aquatic plants is therefore in harmony with Olsen's results with land-plants.

Edaphic Factors.—Charophytes are usually found growing in soft mud at the bottom of ponds and lakes. Occasionally, however, they may be found in soil containing a large percentage of sand, as the specimens of *Nitella acuminata* and *N. mucronata* collected at Mingaladon. Some species appear to flourish best in paddy-fields.

V. ECONOMIC IMPORTANCE.

On the whole, the Charophyta appear to be a group of relatively little economic importance.

Manure.—One of the chief uses appears to be as a form of manure. The decayed remains of the plants from banks are dug up and used as manure in various European countries. According to Prosper (1910), these deposits are collected from lakes and pools in Switzerland, dried, and then spread over the land, and the peculiar odour emitted by the plants helps to keep the soil free from insects. Centesimal composition of *Chara hispida* dried in 'air' according to the same author is as follows :—

Water	5·25
Pure ash and silica	47·00
Crude fat	1·80
Crude protein	4·37
Crude cellulose	7·64
Other carbonic hydrates	33·94

In the ash, for every 1000 parts, 161 are lime and 1·57 phosphoric anhydride. The same authority further claims that experiments with Charophytic manure on various grasses and papilionaceous plants have demonstrated its 'enormous efficacy.'

Samples of *C. zeylanica* and *C. brachypus* from Taunggyi were found to contain as much as 65 per cent. and 47 per cent. calcium carbonate. It is well known that calcium carbonate plays an extremely important part in the soil, and profoundly affects not merely the soil, but also the vegetable relationships. It is used to prevent 'sourness' of soil and to ameliorate dense clayey soils, and 'chalking' and 'marling' is a common agricultural practice in England etc. to renew the calcium carbonate in the soil. Russell (1921) remarks : 'The nature of the plant residues and the ease with which they are decomposed by bacteria depends on climatic factors and also on the amount of calcium carbonate present.'

Charophytes are not used as manure in Burma, but, in view of their abundance, it may be worth while to try them, as they appear to furnish a cheap and useful source of calcium.

In fish culture.—It is believed that Charophytes are useful in fish culture, as some fish make homes in them. This has never been observed in Burma. In France species of *Chara* were used for polishing plate.

As destructive agents of Culicid larvae.—A very important question is the relation of Charophytes to the destruction of mosquito larvae, and many and varied have been the opinions expressed. Blow (1927) came to the conclusion that the Charophyta do not possess any larvicidal properties, and that some other factor or factors must be the cause of absence of mosquito larvae in places where these plants occur. He tested the mosquitoes *Theobaldia annulata* Schr., *Culex pipiens* L., and *Anopheles maculipennis* Mg., with various species

of *Chara*, and also tried the effect of a solution of glucoside prepared from dried *C. zeylanica* from Madagascar, but with negative results.

Matheson and Hinman (1928), on the other hand, experimenting with *C. fragilis*, came to the opposite conclusion. Noticing that for two successive years no mosquito larvae were present in a pond containing *C. fragilis*, they carried out a series of experiments to see whether the Charophyte was responsible for the absence of the larvae. They found that *Culex territans* Wlk. bred in large numbers in wooden pails sunk in the ground, but in pails containing *C. fragilis* eggs were only occasionally laid and the larvae died. *C. fragilis* was next grown in an aquarium with larvae of *Culex pipiens*, *C. territans*, *Aedes vexans* Mg., and *Anopheles punctipennis* Say, but though the conditions seemed otherwise ideal for rapid larval development, the death-rate was almost 100 per cent. Finally, *C. fragilis* was tested under natural conditions in the original pond by enclosing a large number of larvae in cages made of mosquito netting surrounded by two layers of cheese-cloth. After ten days, four adults in all had emerged, and a week later no living larvae or adults were to be found. Aqueous solution of dried *C. fragilis* was also found to have a larvicidal effect. The authors agreed with previous investigation in finding high pH values to be the factor responsible for the destruction of the larvae, but, as they found a marked daily pH cycle in the presence of *Chara* in all the experiments, the range being from 7·6 to 9·4 during the twelve hours from 3 a.m. to 3 p.m., they came to the conclusion that during the process of photosynthesis the plant produces some substance which diffuses into the water and has a destructive effect on mosquito larvae.

In view of the importance of the subject, it was decided to experiment with local species. Accordingly, *C. gymnopitys* was grown in a glass jar, and after it had recovered from the effects of transplantation, experiments were begun. It was also decided to test whether *Nitella* had any larvidical properties, and *N. acuminata* and *N. oligospira* were also grown in culture. Control jars were set up containing water from the ponds in which the plants were originally growing, and also water from the drain from which the mosquito larvae were obtained. Larvae and pupae were introduced into all the jars, which were covered with wire netting to prevent the escape of any emerging adults. The principal species of mosquito used was *Culex fatigans* Wied.

The results of the first series of experiments were as follows :—

Species.	No. of larvae introduced.	No. of pupae produced.	No. of adults produced.	Time taken.	No. of pupae introduced.	No. of adults produced.	Time taken.
C. gymnopitys	24	20	20	8 days	24	24	1-3 days
N. acuminata	24	19	19	9 days	24	24	Do.
N. oligospira	24	0	0	Larvae killed within 24 hrs.	24	24	Do.
Control 1	24	21	21	8 days	24	24	Do.
Control 2	24	20	20	10 days	24	24	Do.

From this it appeared that no effect whatsoever was exercised by any of the plants on the development of the pupae, and none also on that of the larvae in the case of the first two. But *N. oligospira* appeared to have a distinctly lethal effect on the larvae, and this interesting result stimulated further work. The series of experiments was repeated, but again the results were similar, i.e., *C. gymnopitys* and *N. acuminata* showed no larvicidal properties, while *N. oligospira* again appeared to have a quickly lethal effect on the larvae. On carefully inspecting the jar containing the plant, a dragon-fly larva of the subfamily Libellulinae (owing to the immature condition the identification could not be carried further) was found concealed among the branchlets, and as suspicion arose that it might be the agent responsible for the destruction of the mosquito larvae it was isolated in a jar of water and mosquito larvae were introduced. It was then seen that the insect remained motionless till a larva came near, upon which the latter was promptly attacked and eaten : within a few minutes all the larvae had been accounted for. It appeared evident that the insect had been responsible for the destruction of the larvae, and to test the truth of this surmise experiments with larvae were again tried with all the three plants. Here all the pupae produced developed into adults.

This clearly shows that none of the species had any larvicidal properties. It is true that all larvae did not develop, but this must evidently be put down to causes other than the larvicidal properties of the plants, since, even in the controls where there were no Charophytes, the same thing occurred. Later on the jars were left uncovered, and it was found that mosquitoes laid eggs in them freely and that many larvae were produced which eventually pupated and developed into adults.

It is highly probable, therefore, that the supposed larvicidal properties of Charophyta are non-existent. At the same time it appears to be a well-established fact that mosquito larvae are absent from ponds containing Charophytes. Thus Blow (1927) observed that certain waters in Madagascar contained either an abundance of mosquito larvae or of Charophyta, and Matheson and Hinman (1928) also noted the absence of the larvae from the pond containing *C. fragilis*. In my experience, likewise, similar conditions exist in Burma, and ponds containing mosquito larvae do not contain Charophytes and vice versa. To take one example, in Mandalay a pond near the River Shore with an abundant growth of *Eichhornia crassipes* was examined and it was found that no Charophytes were present, while large numbers of mosquito larvae were noticed. In a flooded field in Mandalay from which *Chara* was obtained, however, no larvae were to be seen. This relation between Charophyta and mosquito larvae probably may be explained by supposing that where a larvicidal effect occurs, larvae-eating insects were present. Their presence might easily have passed unnoticed in a dense growth of Charophytes, especially if, as in the above experiment, they possessed a greenish tinge or other protective camouflage. In a subsequent examination of *N. oligospira* under natural conditions some more insects of the same kind were discovered.

These insects may have a particular aptitude for living amongst Charophytes, which often harbour crustaceans and other small organisms that might serve as prey, and this would account satisfactorily for the absence of mosquito larvae from waters containing Charophyta. High pH values may exert a larvicidal effect, but if this be so it is still questionable whether these high values are caused by the presence of Charophytes, since the study of the pH variation of different ponds has shown that high pH values are also found in ponds from which Charophytes are absent.

It is just possible, of course, that the properties of different species, as far as destruction of mosquito larvae is concerned, is different, and this may be an explanation of the contradictory results obtained by various workers. Unfortunately, *C. fragilis*, the species used by Matheson and Hinman, was not available in Rangoon for experimental purposes. If it is really useful in the destruction of mosquito larvae it would be worth while to introduce it to various regions.

VI. KEY TO THE GENERA AND SPECIES.

1. Coronula composed of 10 cells in two tiers ; branchlets usually
furcate ; stem and branchlets ecorticate. (**Nitelleae.**) ...... *Nitella.*
Coronula composed of 5 cells in one tier ; branchlets non-furcate ;
stem and branchlets often corticate. (**Chareae.**) .... 2.
2. Stipulodes absent ; branchlets of 2–3 very long segments ; bract-
cells 1–2, extremely long .... *Nitellopsis.*
Stipulodes always present, though sometimes rudimentary ;
branchlets of 4 or more moderately long segments ; bract-
cells 4 or more, moderately long .... *Chara.*

Key to Species of Nitella.

1. Branchlets in each whorl uniform and in a single series. (**Homoeo-
clemae.**) .... 2.
Branchlets in each whorl of two kinds, smaller accessory branch-
lets being produced above and below the primary branchlets.
(**Heteroclemae.**) .... *N. hyalina.*
2. Dactyls 1-celled. (**Anarthrodactylae.**) .... *N. acuminata.*
Dactyls 2- or more celled. (**Arthrodactylae.**) .... 3.
3. Ultimate cell conical .... 4.
Ultimate cell allantoid .... *N. superba.*
4. Dioecious .... 5.
Monoecious .... 6.
5. Branchlets 1–2 furcate ; dactyls shorter than penultimate rays. *N. globulifera.*
Branchlets 2–3 furcate ; dactyls longer than penultimate rays.. *N. Annandalei.*
6. Dactyls not much abbreviated .... 7.
Dactyls (at least some of them) much abbreviated .... 10.
7. Gametangia present at first furcation .... 8.
Gametangia absent at first furcation .... 9.
8. Apex of ultimate cell dactyl acute ; plant medium-sized....... *N. mucronata.*
Apex of ultimate cell acuminate ; plant very minute.......... *N. batrachosperma.*
9. Fertile whorls with dense mucous cloud .... *N. elegans.*
Fertile whorls without mucous cloud...................... *N. dictyosperma,*

10. Oogonia solitary .... 11.
 Oogonia clustered .... 12.
11. Dactyls not all much abbreviated .... *N. oligospira.*
 Dactyls usually all much abbreviated .... *N. microglochin.*
12. Antheridium often apparently lateral .... *N. burmanica.*
 Antheridium terminal...................................... 13.
13. Dactyls not uniformly abbreviated ; oogonia clustered at base
 of whorls.. *N. polycarpa.*
 Dactyls uniformly abbreviated ; oogonia not clustered at base
 of whorls.. *N. furcata.*

Key to Species of Nitellopsis.

One species .... *N. obtusa.*

Key to Species of Chara.

1. Stipulodes in a single circle. (**Haplostephanae.**) .... 2.
 Stipulodes in a double circle. (**Diplostephanae.**) .... 9.
2. Stem and branchlets entirely ecorticate .... 3.
 Stem corticate, branchlets corticate or ecorticate .... 5.
3. Dioecious .... *C. Wallichii.*
 Monoecious .... 4.
4. Gametangia clustered .... *C. corallina.*
 Gametangia not clustered .... *C. nuda.*
5. Branchlets ecorticate .... 6.
 Branchlets partially corticate ; the lowest segment ecorticate... *C. hydropitys.*
6. Antheridia and oogonia mostly produced at different branchlet-
 nodes .... *C. erythrogyna.*
 Antheridia and oogonia always produced together at the same
 nodes .... 7.
7. Bract-cells well developed .... 8.
 Bract-cells rudimentary .... *C. burmanica.*
8. Oospore brown.. *C. flaccida.*
 Oospore black .... *C. gymnopitys.*
9. Rows of cortical cells of stem twice as numerous as the branchlets.
 (**Diplostichae.**) .... 10.
 Rows of cortical cells of stem thrice as numerous as the branchlets.
 (**Triplostichae.**) .... 12.
10. Secondary cortical cells more prominent than the primary ..... *C. gymnophylla.*
 Primary cortical cells more prominent than the secondary .... 11.
11. Branchlets entirely ecorticate .... *C. Grovesii.*
 Branchlets +corticate..................................... *C. contraria.*
12. Branchlets entirely ecorticate .... *C. Handae.*
 Branchlets +corticate..................................... 13.
13. Lowest branchlet-segment corticate. .. .. *C. brachypus.*
 Lowest branchlet-segment ecorticate . ... *C. zeylanica.*

NOTE ON THE CLASSIFICATION.

The main divisions in the above classification have been made in accordance with Braun's classification as amended by Groves (1924), the latter author having been followed in elevating to the first rank the sections Homoeoclemae

and Heteroclemae (Homoeophyllae and Heterophyllae Braun). The minor divisions have been freely altered to meet the requirements of Burmese plants. It will be noted that in *Chara* the stem and its covering provides the most convenient basis of discrimination, while in *Nitella* the shape, length, and number of cells of the dactyls, and the number and position of the fertile nodes afford important means of distinction between species. Other characters, such as the size of the sex-organs, the presence or absence of a mucous cloud, etc., are also important.

<center>SYSTEMATIC ACCOUNT.</center>

NITELLEAE

Genus 1. NITELLA Agardh, 1824 (emend. Leonhardi, 1863).

Coronula of oogonium of 10 cells in two tiers of 5 ; stem and branchlets entirely without cortex ; branches normally two at a stem node ; branchlets usually furcate ; antheridia terminal ; oogonia lateral ; oospores laterally compressed.

1. NITELLA HYALINA (De Candolle, 1815) Agardh, 1824.

Mentioned by Groves (1924) as having been collected from ' Tataungtoa (?), south of Prome, Lower Burma ' in 1904 by I. H. Burkill, but it has not been again collected, and so a description is not possible. This species is interesting as being the only representative in India and Burma of the section Heteroclemae, having the branches in each whorl in more than one series and of unequal size. The branchlets are in three series, the upper and lower being small, while the middle one is larger and has more furcations. Hence its identification offers no difficulty.

2. NITELLA ACUMINATA Braun, 1849.

Monoecious. Stem about 700 * thick ; internodes as long or little shorter than branchlets. Whorls of 6–7 branchlets. Sterile branchlets long and uni-furcate ; fertile branchlets short, compact, uni-furcate, on special branches. Primary rays more than half the length of entire branchlet. Secondary rays 2–4 in sterile, only 2 in fertile branchlets ; short, particularly in fertile whorls. Dactyls one-celled, apices acuminate. Oogonia and antheridia at furcations of fertile branchlets. Antheridium solitary, terminal, 350 in diameter. Oogonia solitary, geminate or in groups of three ; 480 long, 385 broad, sub-globose ; spiral cells exhibiting 8–9 convolutions ; coronula small, persistent, 40 high and 60 broad at the base. Oospore almost globose, light to dark brown, 280–300 long and 260–280 broad, showing 6–7 ridges terminating in a crest.

Habitat.—In ponds and paddy-fields ; very common.

Distribution.—1. Rangoon (Prome Road Ponds), Feb. 1927, *M. R. Handa*.

　　　　　　　2. Okkyin, Nov. 1928, *B. P. P.*

　　　　　　　3. Mingaladon, Dec.–Feb. 1928, *Des Raj*.

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* All measurements are approx. and given in terms of μ.

A young sterile state of this species (identified by the one-celled dactyls) was collected early in November in a paddy-field at Okkyin. Subsequent to this it was collected several times from ponds along the Prome Road, while particularly good fruiting specimens were obtained from a series of shallow, inter-connected pools at Mingaladon. It was also collected so late as the end of February. Allen (1928) has remarked that this species ' grows very freely in masses during the rains ' : in Burma, though, it was not found in the rainy season, and seemed to flourish only after the monsoon was well past.

It was curious to discover specimens of this species at different stages of development in the same locality. In pools about to dry up the plants were small and stunted, and the fertile branchlets studded with ripe brown oospores, while in deeper pools close at hand very stout specimens were found without any gametangia The life-cycle of the species is obviously greatly influenced by the environmental conditions. The large masses were usually distinct, but occasionally mingled with clumps of *Chara gymnopitys* or *N. mucronata*. The Okkyin specimens were remarkable in that they grew in a paddy-field where the clayey soil was quite different from the fine sand in which it was thriving at Mingaladon.

N. acuminata is the sole representative of the Anarthrodactylae in Burma ; the only other Indian species with single-celled dactyls, *N. mirabilis*, has not yet been recorded.

Several varieties of this species have been described : Braun, for instance, described the var. *Belangeri* from India, characterised by its large size, stout stem, and short end-segments of branchlets and var. *indica* from Java and the Philippines (see H. &. J. Groves, 1912) with a more slender habit and with longer end-segments. Evidently the species is very variable, and, as mentioned above, may exhibit differences in size etc. in the same locality. The specimens, however, agree with the type, the main difference being the larger size of the antheridium in the Burmese plants.

Braun has described a species under the name of *N. Gollmeriana* (1858) distinguished from *N. acuminata* by its smaller size, the short sterile branchlets, and the acute, rather than acuminate, apices of the dactyls. This will probably have to be regarded as a variety, as it differs but slightly from *N. acuminata*, particularly from some of its extreme forms. *N. acuminata* also shows some likeness to *N. flexilis* in the vegetative parts and in the often geminate oogonia, but differs in the smaller size of the sex-organs and the oospore, in the decoration of the oospore, and in the persistent coronula, as well as in the very acuminate apex to the dactyl.

3. NITELLA SUPERBA, sp. n.   (Pl. 8.)

Dioecia.

♂.—Caulis robustus, 500 diametro ; internodia quam ramuli 1–3-plo longiora. Verticilli fertiles sterilibus distincti capita dense mucosa formando. Ramuli verticillorum 5–6 extra-patentes interdum valde inaequales 2–4 furcati. Radii

primarii ½–⅔ vel etiam ¼ ramuli longitudine : radii secundarii 6 ; tertiarii 3–6 quorum unus interdum simplex est ; quaternarii 3–4, vel interdum 6 tribus in radiis quinaribus 3–4 furcatis. Dactyli valde elongati graciles, 2–3 cellulati ; cellula inferior angusta ; cellula ultima quam cellula inferior brevior, interdum fere aequans, allantoida apice mucronata. Antheridia ad furcationes primas et secundas, 450 diametro, breviter stipitata.

♀.—Caulis robustus, saepe dense mucosus ita ut 875 crassus interdum appareat : internodia quam ramuli 2–5 plo longiora. Verticilli steriles ut in ♂ ; verticilli fertiles capita formantes, nubibus irregularibus dense mucosis circumfusa. Ramuli 3-furcati. Oogonia solitaria ad furcationes primas secundas et tertias, primum fere globosa, demum ad apices duos angusta, 300–350 longa (coronula inclusa), 210–245 lata ; cellulae spirales 8–9 convolutas exhibentes ; coronula persistens, 30 alta.

Dioecious.

Male Plant.—Stem somewhat stout, 500 in diameter ; internodes 1–3 times the length of the branchlets. Fertile whorls distinguished from the sterile by forming heads enveloped in dense mucus. Whorls of 5–6 outwardly radiating, sometimes rather unequal branchlets. Branchlets 2–4-furcate. Primary rays ½–⅔ or even ¼ length of branchlet ; secondary rays 6 ; tertiary 3–6, of which one is sometimes simple ; quaternary 3–4, or occasionally 6, in which case 3 are again furcate into 3–4 quinary rays. Dactyls very long and slender, 2–3-celled ; lower cell narrow ; ultimate cell shorter than lower cell, but sometimes almost equal to it in length, allantoid with a mucronate point. Antheridia at first and second furcations, 450 in diameter, shortly stalked.

Female Plant.—Stem stout, often enclosed in mucus, owing to which it may appear as much as 875 thick ; internodes 2–5 times the length of the branchlets. Sterile whorls as in male plant, fertile whorls forming heads densely invested with irregularly shaped masses of mucus. Branchlets 3-furcate. Oogonia solitary, produced at the first, second, and third furcations, at first almost globose, ultimately narrowing at both ends, 300–350 long (incl. coronula), 210–245 broad ; spiral cells showing 8–9 convolutions ; coronula persistent, 30 high. Ripe oospores not found.

Habitat.—In pools and streams.

Distribution.—1. Maymyo, Oct. 1928, *B. P. P.*

2. Taunggyi (time of year uncertain), *M. R. Handa.*

3. Kyaikmaraw (near Moulmein), Nov. 1928, *M. R. Handa.*

This species presents a very striking appearance by reason of its large size and rich velvety olive-green colour, particularly in the female plant, which has a much heavier investment of mucus than the male. The very numerous and extremely slender dactyls also serve to give it a distinctive appearance. Not only the fertile whorls, but often part of the stem and sometimes even the sterile branchlets are enveloped with a mucous coat. It was collected from many parts of Maymyo, and a similar plant without any sex-organs from Taunggyi.

This is evidently the species referred to by Groves (1924) as '*Nitella* sp., *N. myriotricha* Kütz. prox.' He says of this and a plant from Assam, 'Both these plants belong to Braun's section Polyarthrodactylae, and agree in the main with the Australian *N. myriotricha*, having 2–3-celled dactyls with allantoid-mucronate apical cells, being dioecious, and having the female plant forming small fruiting heads enveloped in mucus. There are, however, some minor points of difference between the Australian plant and those from India as well as between the Indian plants themselves. Further specimens of both the latter are desirable in order to arrive at a satisfactory determination.'

The statement as to the differences between the plants is also true of the Burmese specimens. Fortunately, enough material, however, was obtained to draw up a full description, and it has therefore been deemed advisable to name the form. *N. dualis* described from Indo-China, Annam, and vicinity has dactyls with the uppermost cell allantoid, but here the dactyls are only 2-celled.

The specimens from Kyaikmaraw are rather different from those from Maymyo and Taunggyi. The appearance of the male plant is entirely different from that of the plants from the mountains due to the beautiful green colour and the elegant spherical whorls enveloped in clear mucus, through which the orange-coloured antheridia are clearly visible. The female plant, however, is of an unprepossessing appearance, and has a much thicker coat of mucus than the Maymyo and Taunggyi plants.

4. NITELLA GLOBULIFERA, sp. n.   (Pl. **9**.)

Dioecia : plantae ♂ et ♀ similes.

Caulis tenuissimus, 280–320 crassus ; internodia quam ramuli 2–4-plo longiora. Verticilli steriles majores, ramulorum 6–8 patentium 1–2-furcatorum. Verticilli fertiles in capitulis dense mucosis ; ramuli breves 1–2-furcati. Radii primarii $\frac{2}{3}$–$\frac{1}{2}$ quam ramuli breviores ; radii secundarii 6–8, quorum 1–5 iterum furcati sunt, ceteris simplicibus, circa aequales divergentes et extracurvati ; radii tertiarii 4–6 aequales.

Dactyli 2-cellulati, sed cellula ultima saepe decidua est ; cellula inferior apice conica vel rotundata ; cellula ultima parva angusta acuminata, basi saepe bulbosa, 60 longa et ad basin 20 lata.

Gametangia in capitulis densis mucosis : capitula mascula rotundata, foemina plerumque irregularia. Gametangia ad furcationes ambas posita. Antheridium 370 diametro. Oogonium late ellipsoideum, 350 longum (coronula inclusa), 265 latum ; cellulae spirales 9–10 convolutas exhibentes apice elongatae.

Dioecious ; male and female plants similar. Stem very slender ; 280–320 thick ; internodes 2–4 times the length of the branchlets. Sterile whorls larger, of 6–8, 1–2-furcate, outwardly directed branchlets. Fertile whorls in heads with dense mucous cloud ; branchlets short, 1–2-furcate. Primary rays $\frac{2}{3}$–$\frac{1}{2}$ total length of branchlet ; secondary rays 6–8, of which 1–5 are again furcate and the rest simple, of approximately equal length, divergent, and

slightly curved outwards ; tertiary rays 4–6 of equal length. Dactyls 2-celled, but the ultimate cell is often dropped off ; lower cell tapering conically at apex or rounded ; ultimate cell small, narrow, and acuminate, often with a somewhat bulbous base, 60 long and 20 wide at base. Gametangia borne in dense heads enveloped in mucus ; heads of male plant rounded, those of female plant rather irregular. Gametangia produced at both furcations. Antheridium 370 in diameter. Oogonium broadly ellipsoidal, 350 long (incl. coronula), 265 broad ; spiral cells showing 9–10 convolutions, elongating somewhat at the apex. Oospores not observed.

Habitat.—In flowing streams.

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

This is a very small plant, but is very conspicuous by reason of the dense clusters of gametangia, particularly the rounded, antheridia-bearing heads of the male plant from which the plant derives its name. It was collected in Maymyo at the side of a fairly swift-flowing stream, together with other species of *Chara*, mostly *C. nuda*. The male and female plants differ in the characteristic shape of the fertile heads, but are in other respects very similar.

The species may be compared with the next, for there are similarities in the numbers of the branchlets and the secondary rays, and also in that the fertile whorls are enveloped in a dense mucous cloud, but there are differences in the number of furcations, in the diameters of the stem and of the antheridium, and in the length of the penultimate rays, the latter being longer than the dactyls and not *vice versa* as in the next plant.

By reason of its uniformly 2-celled dactyls it falls within the sub-section Arthrodactylae (Diarthrodactylae Braun), and is sharply differentiated from the brachydactylous species by the long dactyls and by having all the furcations fertile. From the rest it is clearly distinguished by being dioecious. The only other dioecious Indian species within this section, *N. dispersa*, may be readily distinguished from the present species by its 4-furcate branchlets.

5. NITELLA ANNANDALEI, sp. n.   (Pl. **10**.)

Dioecia : planta ♂ tantum cognita.

Caulis mediocriter robustus, 600–825 diametro ; internodia quam ramuli 2–5 plo longiora. Verticilli ramulorum normaliter 8, ±incurvatorum 2–3-furcatorum. Radii primarii elongati, quam dimidium totius ramuli longiores ; radii secundarii normaliter 6–8 ; tertiarii 3–6. Dactyli normaliter 6, quam radii penultimati paulum longiores, 2-cellulati ; cellula superior parva acuta. Antheridia ad furcationes omnes posita solitaria, terminalia 375–450 diametro. Verticilli fertiles dense mucosi.

Dioecious. Stem moderately stout, 600–825 in diameter ; internodes 2–5 times the length of the branchlets. Whorls of about 8, more or less incurved, 2–3-furcate branchlets. Primary rays elongated, more than one-half the length of the entire branchlet ; secondary rays usually 6–8 ; tertiary rays 3–6. Dactyls usually 6, slightly longer than penultimate rays ; 2-celled,

upper cell small and acute. Antheridia produced at all furcations, solitary, terminal, 375–450, in diameter. Fertile whorls enveloped in dense mucus.

The female plant was not collected and the above description is of the male plant only.

Distribution.—Yawnghwe River, near head of Inle Valley, Southern Shan States, March 1922, *N. Annandale*.

This plant has already been referred to by Groves (1924), who gave a brief description, but, in the absence of the female plant, did not name it. A slightly fuller description is given here and it has been named, although it is felt that a discussion of its position among the Nitelleae and more particularly its relationship to allied Australian species had best be deferred until such time as more complete material is available. The name was suggested by Mr. Groves.

6. NITELLA MUCRONATA (Braun, 1834) Miquel.

Monoecious. Stem rather slender, 430 thick ; internodes from 1–2 times the length of branchlets. Whorls of 5–7 branchlets ; sterile and fertile whorls similar. Branchlets 2–3 times furcate. Primary rays a little less than half total length of the branchlet . secondary rays 4–6 ; tertiary rays 3–4 ; quaternary rays 3–4. Ultimate rays 2-celled, rarely 3-celled ; lower cell usually rounded at apex , ultimate cell very short and narrow, conical, ending in a point. Oogonia and antheridia produced at all the furcations. Oogonia solitary, 450 long (incl. coronula), 330 wide ; cells showing 8–9 convolutions ; coronula minute, 35 high. Oospore brown with reticulately decorated membrane, 280 long and 230 wide, showing 6–7 thin ridges. Antheridium 250–280 in diameter.

Habitat.—In ponds.

Distribution.—1. Rangoon (Prome Road Ponds), Feb. 1927, *M. R. Handa*.

　　　　　　　　　2. Toungoo, Dec. 1928, *B. P. P.*

　　　　　　　　　3. Mingaladon, Jan.–Feb. 1929, *B. P. P.*

This differs from the type in the slightly larger number of rays and in the smaller fruit. The plant from Toungoo has a much more tufted habit. All the specimens are small or medium-sized. At Mingaladon it was found growing with *N. acuminata* and *Chara gymnopitys*. There is considerable variation in this species, and Allen (1928) remarks that ' *N. mucronata* is a sort of miscellaneous department ; plants that cannot be got to fit in elsewhere and yet do not possess sufficiently pronounced constant differences of their own to warrant the creation of a new species are apt to find a home here.' It has been previously collected from Katha and Kawkareik in 1904 by I. H. Burkill (Groves, 1924).

7. NITELLA BATRACHOSPERMA (Reichenbach, 1830) Braun.

Monoecious. Stem extremely slender, 175 thick, internodes 1–2 times the length of branchlets. Whorls of 6–7 somewhat spreading branchlets. Branchlets 1–2-, rarely 3-furcate. Primary rays $\frac{1}{3}$–$\frac{1}{2}$ the length of the branchlets ; secondary rays 3–6, some of which are simple ; tertiary rays 3–6.

Dactyls long, often more than half entire length of branchlet, uniformly 2-celled. Lower cell of dactyls tapering slightly and rounded at the apex, slightly broader at apex than base of ultimate cell ; ultimate cell narrow, ending in a point, 70 long and 25 broad at the base.   Gametangia at first and less commonly at second furcation.   Oogonia (not quite mature) 280 long (incl. coronula), and 245 wide ; spiral cells showing 8–9 convolutions and lengthening somewhat at the apex ; coronula minute, 28 high and 34 wide at base. Oospores not seen.   Antheridium small, 175 in diameter.

Habitat.—In a flowing stream (found in deep water in Europe and in shallow ' jhils ' in India).

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

This specimen differs from the type in that there are most commonly six branchlets, though seven are occasionally found.   The branchlets are sometimes only uni-furcate, though most commonly bi-furcate.   There was no trace of the mucilaginous investment from which the species derives its specific name. In this connection Groves and Bullock-Webster (1920) remark that ' The gelatinous covering to the sexual organs which gave rise to the specific name is evidently not a constant character in the species and if present in the British plant is very slight.'   Allen (1925) also states about his Indian plant, ' although from its name one would expect this plant to be enveloped in mucus I found none at all.'   Hence it may well be questioned whether the mucous investment occurs at all, and whether the name is not a misnomer.

The plant was collected in Maymyo towards the latter half of October, and, though it was fruiting freely, no ripe oospores were observed.   It was found by chance in a shallow pool of an otherwise swift-flowing stream, mixed with male plants of *N. superba*, in a mass of *Dichotomosiphon*.   Allen (1928) has noted that ' this species is particularly partial to extremely fine mud, such as would not be found in a stream.   The plant had, however, found a very efficient substitute in a mass of decaying filamentous algae, a softer bed than which is hardly possible.'   There is thus a striking resemblance between the habitat of the plant mentioned by Allen and the present specimen. both growing in a mass of filamentous algae in the pool of a swift but shallow stream.

In Ireland *N. batrachosperma* is found in four to six feet of water, so that it is not easy to collect.   But even in shallow water it is very difficult to detect among the algal filaments, for which habitat it appears to show such a partiality.

It appears to be allied to *N. tenuissima*, but is readily distinguished by its producing sex-organs at the first furcation, by the lesser number of furcations of the branchlets, and by the granulate as opposed to the reticulate membrane of *N. tenuissima*.   It also bears some resemblance to *N. gracilis*, but is distinguished by its uniformly two-celled rays.   It is readily identified by its very minute size, the numerous slender dactyls which often exceed half the entire length of the branchlet, and the few times furcate branchlets bearing gametangia at the first furcation also.   There are usually eight branchlets in European plants, but this is evidently not a constant character.

Another plant of this species was also collected at Maymyo at the same time. The habit of this is entirely different from that of the first plant described, and it also differs in the much greater length of the internodes and the shorter branchlets, the dactyls of which are not so long and flexuous.

8. NITELLA ELEGANS, sp. n. (Pl. **11**.)

Monoecia.

Caulis tenuissimus, 160-200 crassus , internodia quam ramuli 2–4-plo longiora. Verticilli steriles ramulis 8 magnis laxis divergentibus 3–4 furcatis. Radii primarii ½–⁴ longitudinem ramulis aequales. Radii secundarii 8, vix ½ longitudinem radiis primariis aequales : radii tertiarii 3–7 : radii quaternarii 4–6 quorum 1–3 iterum in radiis 3 quinariis furcati sunt.

Dactyli 2-cellulati sed interdum quod radius tantum unus in nodo proditur radius ultimus 3-cellulatus apparet : cellula inferior apice paene rotundata quae paullum latior quam basis cellulae ultimae est ; cellula ultima angusta, apice acuta, 50–70 longa, basi 13–20 lata.

Verticilli fertiles parvi nube mucosa circumfusi sed ceteris modis sterilibus similes. Inter verticillos omnino steriles et fertiles, verticilli semi-steriles interdum in ·furcationibus primariis ramulorum projectum breve plenum genitalium ramulo juveni simile edunt.

Gametangia plerumque ad furcationes secundas et tertias sed interdum etiam ad furcationes primas et ultimas posita. Antheridium 175–210 diametro. Oogonium solitarium, 350 longum, 280 latum ; cellulae spirales 8–9 convolutas exhibentes ; coronula parva persistens, 30 alta et basi 50 lata.

Monoecious. Stem extremely slender, 160 ·200 thick : internodes 2–4 times the length of branchlets. Sterile whorls of 8 large, lax, divergent, 3–4-furcate branchlets. Primary rays ½–⅘ the length of branchlet, secondary rays 8, a little more than half the length of the primary rays : tertiary rays 3–7 : quaternary rays 4–6, of which 1–3 are again furcate into 3 quinary rays. Dactyls 2-celled, but sometimes due to only one ray being produced at a node, the ultimate ray appears to be 3-celled ; lower cell tapering slightly and rather rounded at the apex, which is slightly broader than the base of the ultimate cell ; ultimate cell narrow, tapering to a sharp point, 50–70 long, 13–20 wide, at the base. Fertile whorls small, enveloped in a mucous cloud, but otherwise similar to sterile whorls. Between entirely sterile and fertile whorls, semi-sterile whorls bear at the first furcation of some of the branchlets a short outgrowth like a young branch, full of sex-organs. Gametangia at usually second and third furcations, but occasionally at the first and the last furcations also. Antheridium 175–210 in diameter. Oogonium solitary, 350 long, 280 wide ; spiral cells showing 8–9 convolutions ; coronula small, persistent, 30 high and 50 broad at the base. Oospore reddish brown to dark brown, 220 long, 192 wide, almost globose showing 7–8 well-marked ridges.

Habitat.—In ponds.

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

This extremely beautiful species was found in a medium-sized pond in Maymyo, where it formed numerous elegant tufts. It was noticed that the plants tended to grow at short distances from each other and that they apparently preferred solitary to gregarious growth, though there was plenty of room and little competition offered by other plants. The plants varied from two inches to eight inches in height, and extended outward from the very edge of the water-line to a distance of approximately six feet, into a depth of one and a half feet.

The most striking feature of the species is the outgrowth resembling a branch which is frequently found in the axils of the first furcations of the branchlets of the upper whorls. This curious organ is simply studded with antheridia and oogonia, particularly the former. The fertile whorls are sharply distinguished from the sterile ones by their much smaller size and mucous investment. Sterile whorls in the upper region bear a few gametangia, and hence appear to be intermediate between the other two. The large number of secondary rays is another noteworthy feature.

The peculiar outgrowth is a characteristic shared by *N. flagellifera*, a species described from India by Groves and Allen (1927). In this species these special branches are produced at both the first and the second branchlet-node, and there is also a great difference in the size and thickness of the stem, in the number of the branchlets, and in the number of furcations. The presence of a small shoot at the first branchlet-node has been mentioned as occurring in a form of *N. microcarpa* Braun, 1858, from Surinam (Groves & Allen, 1927), but here the oogonia are in clusters, and the dactyls are mostly short and divergent. *N. elegans* may be provisionally assigned a place in the Mucronatae near *N. mucosa*, from which, however, it is sharply discriminated by the different numbers of the branchlets and secondary rays, and by the first node not being usually fertile. Among the Brachydactylae it is nearest to *N. oligospira*.

9. NITELLA DICTYOSPERMA Groves, 1898.

Monoecious. Stem slender or moderately stout, 500 in diameter ; internodes hardly longer than the branchlets. Whorls of six slightly spreading branchlets. Sterile whorls usually with long, 2-furcate branchlets ; primary rays half total length of branchlet : secondary rays 3 : tertiary rays 3. Fertile whorls with 2-3- occasionally 4-furcate branchlets ; primary rays $\frac{1}{3}-\frac{1}{2}$ total length of branchlet ; secondary rays 5-6 ; tertiary rays 3 ; quaternary rays 3-4 ; quinary rays 3. Dactyls all slightly unequal, but not much abbreviated, except occasionally one ; usually 2-, very rarely 3-celled ; lower cell tapering slightly and rounded at the apex ; upper cell 90 long, 30 wide at base, acute or slightly drawn out, base usually much narrower than apex of penultimate cell. Gametangia at the second and third furcations, ultimate node usually fertile. Oogonia 560 long (incl. coronula), 400 wide, light reddish ; spiral cells showing 7-8 convolutions ; coronula small and flat, 40 high, and 70 wide at base. Ripe oospores not found. Antheridium 280 in diameter.

Habitat.—In ponds.

Distribution.—Toungoo, Oct. 1928, *B. P. P.*

The proposers of the species remark that ' this species is closely allied to *N. oligospira*, with which perhaps it should be combined.' The chief difference would appear to lie in the fact that in *N. dictyosperma* the ultimate rays are never regularly shortened, only one being occasionally shortened as in *N. mucronata*, and that the ultimate node is usually fertile, but this is hardly sufficient ground for the creation of a distinct species.

The present plant occasionally has the branchlets 4-furcate as in *N. oligospira*, but it has not been placed under that species, as the mode of shortening of the dactyls has been considered to be a more important character than the occasional extra furcation. It has not been previously recorded from India or Burma.

10. NITELLA OLIGOSPIRA Braun, 1858.

Monoecious. Stem slender, 320–480 in diameter : internodes 1–3 times the length of the branchlets. Whorls of 6–7 straight or slightly spreading branchlets. Sterile and fertile whorls similar, 2–3-furcate ; fertile whorls occasionally 4-furcate. Primary rays ⅓–½ entire length of branchlet ; secondary rays 6–7 ; tertiary rays 2–6, of which 1–3 are usually simple ; quaternary rays 3–4, of which 1–2 are occasionally again furcate into 3 quinary rays. Dactyls variable in length, some much abbreviated . lower cell tapering, rounded or truncate at apex, which is little broader than base of ultimate cell : ultimate cell narrow, acuminate, 90–130 long, 25–30 broad at base Oogonia and antheridia borne at the second and third furcations. Oogonia solitary, ovoid, 500–560 long (incl. coronula), 440–460 broad ; spiral cells showing 7–8 convolutions ; coronula small, persistent. Oospore 350 long, 315 wide, showing 6–7 ridges ; oospore membrane reticulate, light brown. Antheridium 220 in diameter.

Habitat.—In ponds.

Distribution.—Rangoon (Prome Road Ponds), Nov.–Jan. 1928–29, *B. P. P.*

This species and the foregoing, and to some extent *N. polycarpa*, are separated from the remainder of the Brachydactylae by all the dactyls not being abbreviate. It was discovered in Rangoon in considerable quantity, and was successfully cultivated in a glass jar. It has been previously recorded from Pegu (see Groves, 1924).

11. NITELLA MICROGLOCHIN Braun (?).

Monoecious. Stem rather stout, from 400–700 in diameter : internodes usually exceeded in length by the branchlets. Fertile and sterile whorls similar, of 5–7 branchlets. Branchlets rather stout, in sterile whorls usually once, and in fertile 2–4 times furcate. Primary rays ⅓ to more than ½ the entire length of the branchlets : secondary rays 4–5, tertiary rays 3–4 ; quaternary

rays 2–3 ; quinary rays 2–3. Dactyls 2-celled, often very much abbreviated, the lower cell often not much longer than broad. Antheridia and oogonia produced at the first and second furcations. Antheridium 250 in diameter.

Oogonia immature.

Habitat.—Uncertain.

Distribution.—Mergui, 1927, *S. L. Ghose.*

This large species was collected in considerable quantity from Mergui, and though mature fruits were lacking it was identified by the extremely short dactyls, the lower cell being often not much lenger than broad, but this is by no means constant, and the identification is rather dubious. It was originally described by Braun from a specimen collected by S. Kurz in the Kolodyne Valley, Arakan. No other record exists. Groves's opinion (1924) is that it may possibly be merely an extreme form of one of the other species of the Brachydactylae.

12. NITELLA BURMANICA, sp. n.   (Pl. 12.)

Monoecia.

Caulis robustus, 740 crassus ; internodia quam ramuli 2–4 longioribus. Verticilli steriles magni laxi ; ramuli 6–7, 2–3 furcati ; radii primarii elongati ; radii secundarii 3–4 ; tertiarii 2–3. Verticilli fertiles ramulorum 5–6, gracilium brevium, plerumque 4-furcatorum ; radii primarii totam longitudinem ramulorum ½ vel paullum longiores ; radii secundarii 6 ; tertiarii 3–4 ; radii quaterni 3–4 quorum 1–2 multo abbreviati et simplicii sunt ; quinarii 3. Dactyli 2-cellulati, brevissimi ; cellula inferior major ad apicem decrescens quae latitudine basin cellulae terminalis aequat ; cellula terminalis acuta vel leviter acuminata.

Gametangia plerumque ad nodos 3 primarios et basi verticillorum (sed interdum ad nodum quartum) producta.

Antheridium 350 diametro, saepe in visu (sed non vere) laterale. Oogonia ad nodos 2–6, 530 (coronula inclusa) longa, 450 lata ; cellulae spirales 8–9 convolutae ; coronula 60 alta, ad basin 70 lata. Oospora 300 longa, 260 lata, aureo-fusca, late ellipsoidea vel subglobosa, iugis 6 leviter alatis.

Monoecious. Stem stout, 740 thick ; internodes 2–4 times the length of the branchlets. Sterile whorls large, lax ; branchlets 6–7, 2–3-furcate ; primary rays elongated ; secondary rays 3–4 ; tertiary rays 2–3. Fertile whorls of 5–6 short, slender branchlets ; branchlets usually 4-furcate ; primary rays ½ or little more of the entire length of the branchlet ; secondary rays 6 ; tertiary 3–4 ; quaternary rays 3–4, of which 1–2 are much abbreviated and not further divided ; quinary rays 3. Dactyls 2-celled, extremely short ; lower cell longer, tapering towards apex, which is as wide as base of terminal cell ; terminal cell acute or slightly acuminate. Gametangia usually produced at the first 3 nodes and at the bases of the whorls, but also occasionally at the fourth node. Antheridium 350 in diameter, often pushed over to one side. Oogonia 2–6 at a node, 530 long (incl. coronula), 450 broad ; spiral cells showing

8-9 convolutions ; coronula 60 high, 70 wide at the base. Oospore 300 long, 260 broad, golden brown, broadly ellipsoid or subglobose, showing 6 slightly flanged ridges.

Habitat.—In roadside ponds.

Distribution.—Kyaikmaraw (near Moulmein), Oct.–Nov. 1928, *M. R. Handa.*

This plant, which ranges from six inches up to one foot in height, was collected in the last week of October at Kyaikmaraw near Moulmein, but at that time no ripe oogonia or oospores were formed. It was re-collected from the same locality a month later when mature oogonia and a few ripe oospores were found.

The very short dactyls and the clustered oogonia place it in the group of brachydactylous Nitellas to which *N. furcata* and *N. microcarpa* belong.

13. NITELLA POLYCARPA sp. n. (Pl. 13.)

Monoecia.

Caulis robustus, 600 crassus ; internodia quam ramuli 2-3-plo longiora. Verticilli fertiles et steriles similes, ramulorum 6 patentiorum 3–5 furcatorum. Radii primarii totius longitudinis ramulorum $\frac{2}{5}-\frac{1}{2}$; radii secundarii 2–4, tertiarii 2-3 ; quaternii 3, interdum inaequalia, uno plerumque simplici. Dactyli saepe inaequales, interdum omnes abbreviati vel unus duobus ceteris multo longior, 2- (vel interdum 3-) cellulati ; cellula inferior apice truncata . cellula ultima longior vel brevior ad apicem acuta.

Gametangia ad nodos tres primarios. Antheridia ad nodos secundarios et tertiarios, 275 diametro. Oogonia basi verticillorum et ad nodos primarios, secundarios et tertiarios, 2–4 saepe aggregata, sed sola nodo tertiario, late ellipsoidea, 480 longa, 370 lata ; cellulae spirales 7–9 convolutas exhibentes ; coronula magna, 66 alta et basi 52 lata, cellulis saepe inaequalibus divergentibus. Oospora pallide brunnea, subglobosa, iugis minutis 6–7, 260 longa et 250 lata ; membrana subtiliter nodoso-reticulata.

Monoecious. Stem somewhat stout, 600 thick ; internodes 2-3 times the length of the branchlets. Fertile and sterile whorls similar, of 6 spreading, 3-5-furcate branchlets. Primary rays $\frac{2}{5}-\frac{1}{2}$ the entire length of the branchlet ; secondary rays 2–4 ; tertiary rays 2-3 ; quaternary rays 3, sometimes unequal, one often simple ; quinary rays 2-3, which may be again furcate into 2-3 dactyls. Dactyls often unequal, sometimes all being much abbreviated or one being much longer than the other two, 2- occasionally 3-celled ; lower cell truncate at apex ; ultimate cell fairly long or short, tapering to a point : when 3-celled the lowermost cell is much longer than the upper two. Gametangia at first 3 nodes. Antheridium produced at second and third nodes, 275 in diameter. Oogonia at base of whorls and at first, second, and third nodes, in clusters of usually 2–4, though solitary if at the third node ; broadly ellipsoid ; 480 long, 370 broad ; spiral cells showing 7–9 convolutions ; coronula large, 66 high and 52 broad at base, cells often unequal and divergent. Oospore light brown, with finely nodose-reticulate membrane, subglobose, showing 6–7 minute ridges, 260 long and 250 broad,

Habitat.—In shallow water near a swamp.

Distribution.—Toungoo, Oct.–Dec. 1928, *B. P. P.*

This specimen was first discovered in shallow water covering land adjacent to a stretch of swampy land. Owing to the water having become shallow the plants which are fairly tall were not erect, being forced to lie almost prostrate on the ground. A large number of other plants, such as *Marsilia, Azolla,* and Blue-green Algae, were found mixed up with it. Later on other specimens of the same kind were obtained from ponds two to three feet deep from another part of Toungoo.

This species evidently belongs to the brachydactylous portion of the Arthro-dactylae and may be placed between *N. microcarpa* and *N. furcata.* It resembles both, but differs from the former in that the branchlet is occasionally 5-furcate, the oogonia are clustered at the second furcation and the coronula is often elongate. It resembles *N. furcata* in the last-named character, but differs in that the dactyls are not so uniformly abbreviated and the oogonia are clustered at the base of the whorls. It differs from both in the occasional presence of a 3-celled dactyl. It has therefore been deemed appropriate to elevate it to specific rank, placing it between *N. microcarpa* and *N. furcata.*

14. Nitella furcata Agardh, 1824.

Monoecious. Stem moderately stout ; internodes 1–2 times the length of the branchlets. Whorls of 6 outwardly directed, spreading, 3–4-, occasionally 5-furcate, branchlets. Primary rays about ½ the length of the entire branchlet : secondary rays usually 6 : tertiary rays 3–4 ; quaternary rays 2–3, sometimes unequal in length ; quinary rays 2–3, abbreviated or somewhat long and again furcate into 2–3 abbreviated rays. Dactyls 2-celled : lower cell tapering but truncate at apex, which is of same breadth as base of terminal cell ; ultimate cell conical, acuminate, the drawn out tip being sometimes bent to one side, 90 long, 30 broad at base. Antheridium solitary, 280 in diameter. Oogonia clustered, borne at all except the ultimate nodes ; 580 long (incl. coronula), 330 broad ; spiral cells showing 8–9 convolutions : coronula elongate, some or all of the cells being prolonged into a point. Oospore 300 long, 230 broad, dark brown, showing 6–7 ridges.

Habitat.—In ponds, lakes, and paddy-fields.

Distribution.—1. Kamayut, Dec. 1927, *B. P. P.*
2. Rangoon (Victoria Lakes), Nov. 1928, *B. P. P.*
3. Nyaungbinzaik, Nov. 1928, *M. R. Handa.*
4. Okkyin, Nov. 1928, *Des Raj.*

This appears to be a common species in Rangoon and neighbourhood, and is sometimes present in considerable quantity. It was also collected at Nyaungbinzaik near Moulmein, and according to Groves (1924) has been recorded by Braun from Pegu. It is a characteristic species of the Brachy-dactylae with much shortened dactyls and sterile ultimate nodes. The upper cells of the coronula are elongate and divergent, and afford a ready means of identifying the species.

CHAREAE

Genus 1. NITELLOPSIS Hy, 1889.

Coronula composed of 5 cells in a single tier. Stem and branchlets ecorticate. Stipulodes absent. Branchlets of 2–3 very long segments. Bract-cells very long, 1–2 at a node.

1. NITELLOPSIS OBTUSA (Desvaux, 1810) Groves.

Sterile specimens which have been referred to this species by Groves (1924) were collected in 1892 from Fort Stedman, Upper Burma, by Abdul Huk : it has not been collected since. This species, the only one in the genus, is remarkable for producing bulbils of a symmetrical star-like form representing metamorphosed branchlet-whorls, hence the very appropriate specific name ' *stelligera*,' which had to be abandoned in accordance with the rules of nomenclature.

Genus 2. CHARA Linnaeus, 1754 (emend. Agardh, Leonhardi, and Braun).

Coronula of 5 cells in a single tier. Cortex often present. Stipulodes present, though sometimes rudimentary. Branchlets of 4 or more segments ; bract-cells 4 or more at a node. Oogonia and antheridia produced one above the other from periphery of branchlet-nodes, antheridium below the oogonium. Oospore terete in section.

1. CHARA WALLICHII Braun.   (Pls. **14** & **15**.)

Dioecious, male and female plants similar. Stem stout, 875 thick : internodes usually exceeded in length by the branchlets. Cortex entirely absent. Stipulodes rudimentary. Branchlets 5–6, nearly straight, of 4–6 segments, the lower 3–5 elongated, the ultimate segment short, scarcely longer than the surrounding bracts, or fairly long, conical. Bract-cells variable in number, commonly 3–4, moderately long. Bracteoles usually 3, similar to bracts, very slightly exceeding fruit in length. Gametangia produced at the base of the whorls as well as at the branchlet-nodes. Oogonia clustered both inside and outside the branchlets and at the first branchlet-node, where 1–2 usually occur ; broadly ellipsoid, 840–900 long (excluding coronula), 630–700 broad, the spiral cells showing 7–8 convolutions ; coronula straight, persistent, 140–155 high, 200–235 broad at the base. Oospore broadly ellipsoid to ellipsoid-cylindrical, truncate at the base, about 610 long, 440 broad (excluding ridges), almost black, showing 6–7 prominent ridges terminating in short claws ; outer membrane thick, black, opaque. Antheridia clustered at the bases of the whorls, both inside and outside the branchlets, and at the first and second branchlet-nodes, usually 2–3 at the former and 1–2 at the latter ; 790–875 in diameter.

Habitat.—In a small pond 3–4 feet deep.

Distribution.—Toungoo, Dec. 1927–1928, *B. P. P.*

A large plant with a somewhat tufted habit. Its outstanding features are the entire absence of cortex, the long segments of the branchlets, the well-developed bract-cells, the rudimentary stipulodes, and the characteristic terminal segment. This last is sometimes not much longer than the bract-cells at the ultimate node, forming a coronula-like termination to the branchlets. The fact that the gametangia are produced at the base of the whorl as well as at the branchlet-nodes is noteworthy, as it constitutes a fundamental point of discrimination between this species and *C. Braunii* Gmelin (1826) and *C. nuda* (described in the following pages), where the oogonia and antheridia are produced only at the branchlet-nodes. Though also near to *C. corallina*, it is readily distinguished from the latter in having a dioecious habit, well-developed bract-cells, and in the smaller fruits.

The present plant differs from the type in that no oogonia were noticed at the second branchlet-node. This species was originally described from a male specimen collected in India in 1809, and the only other records of it are by Allen (who found both male and female plants) from the United Provinces in 1922 and 1923. Hence the occurrence of this rare species in large quantity in Burma possesses considerable interest.

2. CHARA CORALLINA Willdenow, 1803.

Monoecious. Stem stout, 800 thick ; internodes elongated, often attaining a length of about 6 inches in the older parts. Cortex entirely absent. Stipulodes small, acute, occasionally well developed in younger whorls, but usually rudimentary. Whorls of usually 8 branchlets. Branchlets of about 4 swollen segments, the ultimate one being very short, acute with often a rather bulbous base. Bract-cells 3–4, very small, acute, never developed on the ultimate node. Gametangia produced at the base of the whorls as well as at the branchlet-nodes. Antheridia and oogonia very young.

Habitat.—In ponds.

Distribution.—Hsipaw (Northern Shan States), Oct. 1928, *Ba Nyan.*

A very large and robust plant, growing in clumps. The specimens consisted largely of the lower portions of the plants only, and these are characterised by the much elongated internodes. There is a well-marked annular incrustation in the form of a series of bands alternating with the clear green unincrustated areas. When young the somewhat swollen branchlets tend to close together, though in the older parts they diverge freely. Unfortunately, gametangia in only the youngest stages of development were to be seen.

This species is separated from *C. Wallichii* by the larger fruits and by its monoecious character, and from *C. Braunii* and *C. nuda* by the production of gametangia at the base of the whorls as well as at the branchlet-nodes. It was collected once before from Burma by I. H. Burkill from Kyantaw, District Akyab, in 1907 (Groves, 1922).

3. CHARA NUDA, sp. n. (Pl. 15.)

Monoecia.

Caulis gracilis, 350 crassus, omnino ecorticatus. Internodia plerumque brevia, quam ramuli breviora. Stipulodia in serie una, plerumque inchoata, acuta. Verticilli ramulorum 7–8 incurvatorum ecorticatorum 5-segmentorum : cellula ultima angustior et plerumque brevior apice acuta. Bracteae inchoatae. Bracteoli graciles, acuti, longitudinem a dimidio ad totum fructum variabiles.

Gametangia at nodos duos inferiores edita. Antheridium parvum, 230 latum. Oogonia 800 longa, 525 lata ; cellulae spirales 14-convolutae ; coronula 70 alta, basi 190 lata, brevis, complanata et conniventia interdum inter coronulum et cellularum spiralium apices leviter constricta. Oospora ovalia-ellipsoidea, nigra, 450 longa, 330 lata, iugis parvis 12 in unguibus brevibus basalibus terminatis.

Monoecious. Stem slender, 350 thick, entirely ecorticate. Internodes usually short, exceeded in length by the branchlets. Stipulodes in a single row, usually rudimentary, acute. Whorls of 7–8 incurved branchlets. Branchlets ecorticate, of usually 5 jointed branchlets, terminal cell narrower and shorter, tapering to an acute point. Bracts rudimentary. Bracteoles slender, acute, varying in length from one-half to as long as the fruit. Gametangia at the two lowest nodes. Antheridium small, 230 broad. Oogonia 800 long, 525 broad ; spiral cells showing about 14 convolutions ; coronula 70 high, 190 broad at the base, short, flattened, and connivent, with sometimes a slight constriction between it and the apices of the spiral cells. Oospore oval-ellipsoid, black, 450 long by 330 broad, showing about 12 low ridges ending in short basal claws.

Habitat.—In a swift-flowing stream.

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

A small plant usually not exceeding six inches in height, heavily incrusted with lime. This is another addition to the group of ecorticate haplostephanous Charas, of which three have been recorded from India. It is readily distinguished from *C. Wallichii* and *C. corallina* by the unclustered gametangia, for as in the remaining species, *C. Braunii* (which has not yet been recorded from Burma), the sex-organs are solitary. From *C. Braunii* it is distinguished by the smaller size, by the acute, usually rudimentary stipulodes, by the lack of a corona-like termination to the branchlets, by the always solitary sex-organs, and by the larger size of the fruit whose spiral cells also show a larger number of convolutions.

4. CHARA HYDROPITYS Reichenbach, 1834.

Monoecious. Stem rather slender, 480 thick ; internodes 1-4 times the length of the branchlets. Stipulodes in a single series, long and acute. Cortex variable, usually diplostichous, sometimes triplostichous. Spine-cells solitary, rudimentary. Whorls of usually 11 spreading branchlets. Branchlets of

5–7 segments, the lowest and some of the uppermost segments ecorticate, the intervening segments corticate. Bract-cells about 8, long and acute. Bracteoles like the bracts, 1½–2 times the length of the fruit. Oogonia and antheridia produced at the 4 lowest nodes, i.e., above the corticate segments also. Antheridium 210 in diameter. Oogonia 500 long, 330 broad, ellipsoid ; spiral cells showing 13–14 convolutions ; coronula 60 high, 100 wide at the base. Oospore 315 long, 230 broad, oval-ellopsoid, showing 12–13 low ridges terminating in very short basal claws ; oospore-membrane black.

Habitat.—In roadside ponds and in paddy-fields.

Distribution.—1. Toungoo, Oct. 1928, *B. P. P.*

2. (?) Mandalay, 1927, *B. P. P.*

The specimens of this species were obtained in isolated clumps in roadside ponds and in cuttings left after digging out earth to build up embankments for a road, and which were filled by water in the rainy season. It was rather difficult to detect, as it was almost obscured by the masses of *Utricularia*, which were plentiful in the shallow pools. The specimens agree fairly well with the type, differing in the absence of an eighth segment, in the smaller size of the fruit, and in the fact that the fourth node is occasionally fertile. This is the first record for Burma, though Braun recorded it from Bengal and Madras, and Allen from Gonda.

A few fragments of a plant gathered at Mandalay without mature fruit have been also provisionally referred to this species, though considerable differences exist. The plant is more robust, the cortex is triplostichous. with the primary series more prominent than the secondary, the bracts are rudimentary, and only 1–2 branchlet-segments, viz., the second and sometimes the third from the base, out of the total six, are corticate. Oogonia and antheridia are usually situated at the first two nodes only. In the absence of sufficient material, and particularly in the lack of ripe fruit, the further determination of the specimen is impossible, and must be deferred till such time as it is re-collected.

5. CHARA ERYTHROGYNA Griffith.

Monoecious. Stem rather slender, 500 in diameter ; internodes 1–2 times the length of the branchlets. Stipulodes in single row, elongated, with acute or slightly acuminate apices. Cortex diplostichous, cells of the primary series more prominent than those of the secondary series. Spine-cells rudimentary or well developed. Whorls of usually 13 branchlets. Branchlets very slender, of about 6 segments ; entirely ecorticate. Bract-cells 6–8, long, acute. Bracteoles twice the length of the fruit. Oogonia and antheridia usually situated at different nodes, the oogonia more commonly at the upper nodes. Antheridium 250–315 in diameter, often 2 together. Oogonia 560 long (excluding coronula), 350 wide ; spiral cells showing 9–10 convolutions ; coronula 40–45 high, 105 wide at base. . Oospore 400 long, 245 broad, black, showing 8–9 ridges.

Habitat.—In roadside drains and in lakes.

Distribution.—1. Rangoon (Victoria Lakes), 1927, *S. L. Ghose.*

2. Maymyo, Oct. 1928, *B. P. P.*

The specimen from Victoria Lakes, on which the above description is based, is a delicate-looking plant of diminutive size. The Maymyo plant is more robust, and differs in that the spine-cells are very well developed, being two to three times the diameter of the stem in length, whereas in the Rangoon plant they are rudimentary. In Maymyo the specimen was discovered growing in a ditch at the side of a road in company with *C. gymnopitys*. *C. erythrogyna* is a member of a group of three Charas recorded from India which possess a single row of stipulodes, and a corticate stem, but entirely ecorticate branchlets, and is distinguished by the fact that the oogonia and antheridia are rarely produced at the same branchlet-node, as in *C. flaccida* and *C. gymnopitys*. *C. burmanica*, which is described below, is also haplostephanous, and possesses a corticate stem and ecorticate branchlets, but has rudimentary bracts and spine-cells, and differs markedly in appearance from the present species.

The plant is very conspicuous when fruiting, due to the striking red colour of the sex-organs—from which fact it derives its specific name. The type-species has a whorl of from thirteen to sixteen branchlets of six to eight segments, but in the present specimens not more than thirteen branchlets of not more than six segments were observed—a fact also noted by Allen (1928) in connection with his record of this species from Saharanpur.

This is its first record for Burma. The Indian records are few and limited chiefly to the northern plain. Outside India it has been recorded from Cochin China and Java.

6. CHARA BURMANICA, sp. n. (Pl. **16**.)

Monoecia.

Caulis gracilis, 430 diametro ; internodia quam ramuli plerumque breviora. Verticilli ramulis 10–12 valde incurvatis. Ramuli graciles 5-segmenti omnino ecorticati. Stipulodia parva obtusa sed fere acuta interdum irregularia, in serie una. Cortex diplostichus ; cellulae serierum primariarum et secundariarum aequaliter prominentes. Cellulae bractearum inchoatae.

Bracteoli ½–1½ longitudini fructus aequales. Gametangia ad duos nodos inferiores ramuli edita. Antheridum 280 diametro. Oogonium 825 (coronula inclusa) longum, 545 latum ; cellulae spirales, 13–14 convolutas exhibentes ; coronula recta, 70 longa et basi 140 lata. Oospora 700 longa, 450 lata, costis 11–12 in unguibus brevibus basalibus terminatis. Membrana oosporae nigra opaca.

Monoecious. Stem slender, 430 in diameter ; internodes usually exceeded in length by the branchlets. Whorls of 10–12 strongly incurved branchlets. Branchlets entirely ecorticate, slender, of 5 segments. Stipulodes small, blunt, but almost acute, sometimes irregular, in single row. Cortex diplostichous ; cells of primary and secondary series equally prominent. Spine-cells lacking. Bract-cells rudimentary. Bracteoles ½ to 1½ times the length of the fruit. Gametangia produced at the two lowest branchlet-nodes.

Antheridium 280 in diameter. Oogonium 825 long (incl. coronula), 545 broad ; spiral cells showing 13–14 convolutions ; coronula straight, 70 high and 140 broad at the base. Oospore 700 long, 450 broad, showing 11–12 ridges terminating in short basal claws. Oospore membrane black, opaque.

Habitat.—In shallow drains and marshy areas.

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

This species, which was growing in very characteristic tufts in shallow drains and marshy land, is whitish, due to much incrustation, and exceedingly brittle. The strongly incurved branchlets without bracts give a distinctive appearance to the plant. The single row of stipulodes places the plant in the Haplostephanae, and the corticate stem and ecorticate branchlets suggest that it is nearly allied to *C. flaccida* and *C. gymnopitys*, with which it also agrees in the number of branchlet-segments. It is readily distinguished from these, however, by the entire absence of bract-cells and spine-cells, and by the much larger fruits. These differences have been considered important enough to justify its being regarded as a new species.

7. CHARA FLACCIDA Braun, 1849.

Monoecious. Stem slender, 450 in diameter : internodes 1–3 times the length of the branchlets. Whorls of 11–12 spreading branchlets. Branchlets of usually 5 segments, ecorticate. Stipulodes in single row, short or elongated, acute. Cortex of stem diplostichous, primary series of cells more prominent than the secondary series. Spine-cells rudimentary. Gametangia produced at the three lowest nodes. Antheridium 300 in diameter ; oogonia ovoid, 580 long (incl. coronula), 455 wide ; spiral cells showing about 9 convolutions ; coronula short, 40 high and 140 broad at base. Oospore 420 long by 315 broad, golden brown to dark brown, showing about 9 ridges.

Habitat.—In pools or ponds.

Distribution.—Rangoon (Prome Road Ponds), Dec. 1928, *B. P. P.*

This species is indistinguishable from the next species, *C. gymnopitys*, with the exception of the colour of the oospore, which is black in the latter and golden brown in *C. flaccida*. In some forms of *C. flaccida*, however, the colour is dark brown, and this is so in the present specimen. Very probably it should be regarded as a subspecies of *C. gymnopitys*.

8. CHARA GYMNOPITYS Braun, 1852.

Monoecious. Stem moderately stout, 500 thick ; internodes 1–4 times the length of the branchlets. Whorls of 10–11 branchlets. Branchlets spreading, of 5 segments, entirely ecorticate. Stipulodes well developed, in a single row. Cortex diplostichous, primary series more prominent than the secondary series. Spine-cells solitary, fairly well developed, not exceeding the diameter of the stem in length. Bract-cells 6–8, long, usually exceeding the segment in length. Bracteoles similar to bract-cells, exceeding fruit in length. Gametangia usually at the two lowest, occasionally at the third node. Antheridium 280 in diameter. Oogonia 580–620 long (incl. coronula), 385–400 broad ;

spiral cells showing 10-11 convolutions ; coronula straight, persistent, 60 high, 110 broad at the base. Oospore 380-450 long, 230-280 broad, showing 9-10 ridges terminating in short basal claws ; membrane black.

Habitat.—In drains, ponds, and paddy-fields. Very common.

Distribution.—1. Taunggyi, Oct. 1927, *M. R. Handa.*

        2. Maymyo, Oct. 1928, *B. P. P.*

        3. Mandalay.

                (*a*) In moat and paddy-fields, Oct. 1928, *B. P. P.*

                (*b*) Agricultural College Farm, Oct. 1928, *H. C. D. Pal.*

                (*c*) Agricultural College Farm, Dec. 1928, *D. Rhind.*

        4. Okkyin, Nov. 1928, *Des Raj.*

        5. Rangoon (Prome Road), Dec. 1928, *B. P. P.*

        6. Mingaladon, Jan.-Feb. 1929, *B. P. P.*

This is apparently the most widely distributed species of *Chara* in Burma. In Mandalay it appeared to form a veritable carpet in some paddy-fields, and was also discovered in the Mandalay moat. The specimens from Mandalay showed a well-marked annular incrustation. The specimens from Maymyo and Taunggyi, though densely coated, showed uniform incrustation, and the same was true of the specimens from Rangoon. Round about Rangoon it was very common, being collected from paddy-fields at Okkyin along with *N. acuminata* and *N. furcata* and in some ponds along the Prome Road.

In appearance it is like *C. hydropitys* or *C. erythrogyna*, particularly the latter. From the former it is readily distinguished by its entirely ecorticate branchlets, and from the other in the lesser number of branchlets and branchlet-segments, and by the oogonia and antheridia being produced at the same branchlet-nodes. It is discriminated from *C. flaccida* by the black colour of the oospore, the former having golden-brown oospores.

9. CHARA GYMNOPHYLLA Braun.

Collected from several places in the Southern Shan States by N. Annandale in 1922. This species is nearly related to and closely resembles *C. vulgaris* Linnaeus, 1753, but is discriminated by the more or less ecorticate branchlets, and by the gametangia being produced at nodes not giving rise to a cortex.

10. CHARA GROVESII, sp. n. (Pl. 17.)

Monoecia.

Caulis mediocriter robustus, 450-700 diametro ; internodia quam ramuli 1-5 plo longioribus. Stipulodia valde evoluta biseriata, obtusa, longitudinem variabilia et inaequalia. Cortex diplostichus ; verticilli ramulis 9-10 omnino ecorticatis, patentibus vel incurvatis 5-6-segmentis. Cellulae bractea normaliter 5, inaequales, media longissima, saepe etiam ½ longitudinem ramulis aequalia, apice obtusae. Bracteoli quam fructus longiores.

Gametangia ad nodos duos inferiores. Antheridium 450 diametro. Oogonia 740 (coronula inclusa) longa, 525 lata ; coronula 90 alta, 230 basi lata ; cellulae spirales 14-15 convolutas exhibentes.

Monoecious. Stem moderately stout, 450–700 in diameter ; internodes 1–5 times the length of the branchlets. Stipulodes well developed in two series, blunt, somewhat variable, and unequal in length. Cortex diplostichous, exhibiting strong torsion. Whorls of 9–11 entirely ecorticate branchlets, spreading or incurved. Branchlet of 5–6 segments. Bract-cells, usually 5 developed, of unequal length, the middle ones very long, often attaining $\frac{1}{3}$ of the length of the entire branchlet ; apices obtuse ; absent on the 2 upper-most nodes. Bracteoles exceeding fruit in length. Gametangia produced at the two lowest nodes. Antheridium 450 in diameter. Oogonia 740 long (incl. coronula), 525 wide ; coronula 90 high, 230 broad at the base, spiral cells showing 14–15 convolutions.

Ripe oospores not observed.

Habitat.—In streams and pools.

· *Distribution.*—Maymyo, Oct. 1928, *B. P. P.*

This species was very common at Maymyo and emitted a disagreeable odour. The very long internodes and the long bracts give it a distinctive appearance, and by the naked eye it might be mistaken for a *Nitella.* In general, it bears some resemblance to *C. burmanica* and *C. Handae*, particularly in the corticate stem and ecorticate branchlets ; it is readily separated from the first by its diplostephanous character and from the second by its diplostichous cortex. It has a position near *C. contraria*, but is distinguished by having entirely ecorticate branchlets.

11. CHARA CONTRARIA Kützing, 1845.

This species has been recorded once from the Northern Shan States, and has the cortex regularly diplostichous, the primary series being more prominent than the secondary. This last character, as well as the usually distinctly irregular stipulodes, serves to distinguish it from *C. vulgaris,* which it resembles.

12. CHARA HANDAE sp. n. (Pl. 18,)

Monoecia.

Caulis mediocriter robustus ; internodia quam ramuli saepe breviora. Verticilli ramulis 9–11 incurvatis. Ramuli segmentorum 5 omnino ecorti-catorum. Stipulodia acuta, biseriata, superiora. Cortex triplostichus ; series primaria quam secundia prominentior. Aculei valde evoluti, solitarii, acuti, aequales diametro caulis longitudine ; cellulae bracteae 4–8 graciles acutae. Bracteoli 1½ longitudini fructus aequales. Gametangia ad tribus nodos inferiores. Antheridium parvum, 350 diametro. Oogonia 875 (coronula inclusa) longa, 615 lata. Cellulae spirales 15–16 convolutas ; coronula recta, 105 alta, basi 190 lata. Oospora 615 longa, 400 lata, ovoideo-cylindracea iugis 13–14 in unguibus brevibus basalibus terminatis ; membrana nigra opaca.

Monoecious. Stem moderately stout, internodes often exceeded in length by the branchlets. Whorls of 9–11 incurved branchlets. Branchlets of 5 entirely ecorticate segments. Stipulodes in double row, acute, those of upper series slightly better developed. Cortex triplostichous ; primary series more prominent than the secondary. Spine-cells well developed, of

about the same length as the diameter of the stem, solitary, acute. Bract-cells 4–8, fairly well developed except on the uppermost node, slender and acute. Bracteoles 1½ times the length of the fruit. Gametangia at the 3 lowest nodes. Antheridium small, 350 in diameter. Oogonia 875 long (incl. coronula), 615 broad ; spiral cells showing 15–16 convolutions ; coronula straight, 105 high, 190 broad at the base. Oospore 615 long, 400 broad, ovoid-cylindrical, showing 13–14 ridges terminating in short basal claws. Oospore membrane black, opaque.

Habitat.—In a stream.

Distribution.—Maymyo, Oct. 1928, *B. P. P.*

This species has a bushy appearance due to the short internodes and the long branchlets, and though the plants are small the fruit is comparatively very large. It was found growing with other Charophytes at the edge of a swift-flowing stream. It is separated from the other Indian and Burmese representatives of the Triplostichae by its entirely ecorticate branchlets.

13. CHARA BRACHYPUS Braun, 1849.

Monoecious. Stem moderately stout, 450 thick ; internodes 1–2 times the length of the branchlets. Stipulodes in double series, well developed, acute. Cortex triplostichous, cells of the primary and secondary series equally prominent. Spine-cells small, solitary, acute. Whorls of 9–11 branchlets. Branchlets incurved, of 6 corticate segments, the lowest of which is very short. Bract-cells 6–7, unequally developed. Bracteoles exceeding the bract-cells. Oogonia and antheridia produced at the 3 lowermost nodes. Antheridium 380 in diameter. Oogonia 830 long, 615 broad ; spiral cells showing 13–15 convolutions : coronula 115 high, 245 broad, slightly spreading. Oospore black, 770 long, 560 broad, showing 12–13 ridges.

Habitat.—In drains, flooded fields, and ponds.

Distribution.—1. Taunggyi, 1927, *M. R. Handa.*

2. Maymyo, Oct. 1928, *B. P. P.*

This species was found to be common at Taunggyi, and was also plentiful at Maymyo, where it was discovered in shallow drains and slightly flooded fields, forming dense matted masses, the plants being short and compact, not exceeding six inches in height. The description was based mainly on the Taunggyi specimens, which were much taller with longer internodes. Apart from the size of the plant, the Maymyo specimens had slightly longer though narrower oogonia than those from Taunggyi. The plants were extremely brittle and, as Allen has remarked, seem to be partial to a firm soil.

This species is confined to the tropical regions, and has a much more restricted distribution than *C. zeylanica.* It is distinguished from the other Indian members of the Triplostichae as follows :—From *C. infirma* Braun it is separated by being monoecious ; from *C. fragilis* by the very short lowest branchlet-segment, by the rows of cortical cells of the branchlets being three times as numerous as the bract-cells, and by the better-developed stipulodes and spine-cells ; from *C. zeylanica* it is distinguished by the lowest branchlet-segment

being corticate. It appears to have been the first Charophyte recorded from Burma, having been collected as long ago as 1890 in Sagaing by Abdul Huk, but there seems to have been no subsequent record of it till the present one, nearly forty years later.

14. CHARA ZEYLANICA Willdenow, 1803.

Monoecious. Stem stout, firm, 700-800 thick, heavily incrusted, internodes 1-3 times the length of the branchlets. Stipulodes in two series, well developed, acute. Cortex triplostichous, cells of the primary and secondary series equally prominent. Spine-cells elongated, acute, solitary. Whorls of 11-12 rather stout, spreading branchlets. Branchlets of 9-11 segments, the lowest segment very short and ecorticate. Terminal segment short, hardly exceeding the bracts. Bract-cells 7-8, anterior ones better developed than the posterior. Bracteoles 3-4 times the length of the bract-cells, exceeding the fruit in length. Gametangia produced from the second up to the fifth branchlet-nodes. Oogonia 875 long (excl. coronula), 560 broad ; spiral cells showing 14-15 convolutions ; coronula slightly spreading, 125 high and 265 broad at the base. Oospore 660-700 long, 330-350 broad, showing 12-14 small ridges prolonged into short basal claws ; membrane black.

Antheridium 450 in diameter.

Habitat.—In moats and ponds.

Distribution.—1. Between Heho and Taunggyi, Oct. 1927, *M. R. Handa.*
        2. Mandalay (moat), Oct. 1928, *B. P. P.*

C. zeylanica is one of the most wide-spread species of *Chara.* Groves remarks that ' *C. zeylanica* in one or other of its many forms is very widely distributed in the tropical and sub-tropical regions of both hemispheres.' It appears to be extremely variable, and many of its varieties were formerly described as distinct species, though later recognised as merely the extreme forms of this species. The present specimen agrees with the forma *Humboldtii* described by Groves (1912 *a*) as follows :—

' Plant usually robust, spine-cells often longer than the diameter of the stem. Branchlets usually 11-12, with 9-11 segments, of which the last (rarely more) is ecorticate. Bract-cells whorled, anterior longer than, posterior half as long as, the oogonium. Oogonia not produced at the lowest node.' It differs from the forma *Berteroi* by the longer spine-cells, the longer bract-cells, and the lesser number of ecorticate segments, and from the forma *Michauxii* by the lesser number of branchlets and the well-developed whorled bract-cells. From the other forms it is distinguished by not producing oogonia at the first node. This last-mentioned character is used in the key in Braun and Nordstedt's ' Fragmente ' (1882) to divide the numerous varieties of this species into two main classes, but it is evidently not constant, as Groves has described plants from Dikwella (Ceylon) in some of which fruits are produced at the lowest node, while in others they are not.

C. zeylanica belongs to a group of about four triplostichous species recorded from India and is near *C. brachypus*, from which it is distinguished by the

ecorticate lowest segment—a peculiarity it shares with the haplostephanous and otherwise quite different *C. hydropitys.*

Another, but quite different-looking, variety was obtained from the Moat at Mandalay, but unfortunately proved to be quite sterile. This was a slender form with minute spine-cells, nine to eleven branchlets of five to nine segments, the lowest and uppermost of which were very short, while the lowest and sometimes the second lowest, as well as the last two to three segments were ecorticate. The bract-cells were about six. This agrees most nearly with forma *elegans,* though differing in the sometimes lesser number of the segments and the fewer bract-cells. The appearance is striking, due to the annular incrustation, the broad whitish bands alternating with the green uncoated areas.

Summary and Conclusions.

Technique and methods.

(1) Although successful herbarium-mounts can be made, it is preferable to preserve some parts at least of the specimens in formalin for purposes of identification.

(2) As a result of trials with a number of fixatives, hot alcohol, and chromo-acetic acid are recommended for use with Charophyta.

(3) Formalin (2 per cent.) and alcohol (90 per cent.) are useful preservatives.

(4) Nitric acid is useful for decalcifying the incrusted species.

(5) For glycerine preparations, alum carmine and Heidenhein's Iron Haematoxylin were the most useful stains. Magdala Red is pleasing, but tends to run out in the glycerine.

(6) For balsam preparations the above-mentioned stains and safranin and gentian violet as well gave good results.

Distribution.

(1) A promising field awaits the investigator of Charophyta, a good number of new records and nine new species having been discovered in a comparatively short space of time, in spite of the difficulties in the way of collection.

(2) The hills have yielded a richer Charophyta flora, both as regards quantity and number of species, than the plains.

(3) The Chareae are usually to be found both in the hills and the plains, but the species of the Nitelleae are usually confined to the hills only or to the plains.

(4) The best season for the growth of Charophytes is between the months of August and March.

(5) Few species flourish throughout this period, many appearing and dying off early, while others appear later on in the season.

(6) A brief account of the climate of the chief centres of collection is given.

Ecology.

(1) Observations on the aquatic flora, particularly algae, with reference to the succession of forms, suggest that during the dry season and the early part of the monsoon the non-cellular or colonial algae are most prominent, but soon give way to the filamentous forms as the monsoon progresses. In Rangoon, Charophytes do not make an appearance till towards the end of October.

(2) General observations were made on the Charophytes as an aquatic community and their relationship with other aquatic plants discussed.

(3) The influence of the various ecological factors is noted.

(4) The influence of a hitherto uninvestigated factor, viz., the pH of the habitat, is considered in detail and an account given of the variation in pH of the water of Rangoon ponds. The conclusion is reached that high pH is favourable to the growth of Charophytes, while a pH below a certain limit (about 8·0) inhibits their growth.

Economic importance.

(1) As manure the Charophytes appear to supply a cheap and efficient means of enriching land. The amount of $CaCO_3$ present was investigated in a few Burmese plants.

(2) Investigations carried out with three species of Charophytes with uniform numbers of mosquito larvae and pupae, and with suitable controls, established that there is no larvicidal effect. An apparent larvicidal effect in one species was found to be due to the presence of a larvae-eating insect.

(3) Some of the previous results on the larvicidal effects of Charophytes are discussed and an explanation suggested to reconcile the conflicting observations.

Systematic account.

(1) A key to Burmese species is given.

(2) Twenty-five species have been described, including ten new species. This, with four previous records from Burma which were not re-collected, makes the large total of three genera and twenty-nine species for Burma. (The total number of species described from the whole of India in Groves's ' Notes on Indian Charophyta ' is thirty-six.)

(3) Original drawings are given of all the new species, as well as of the rare and interesting *C. Wallichii.*

(4) Notes on the appearance and mode of growth of each species are given, and the position of each in the group discussed.
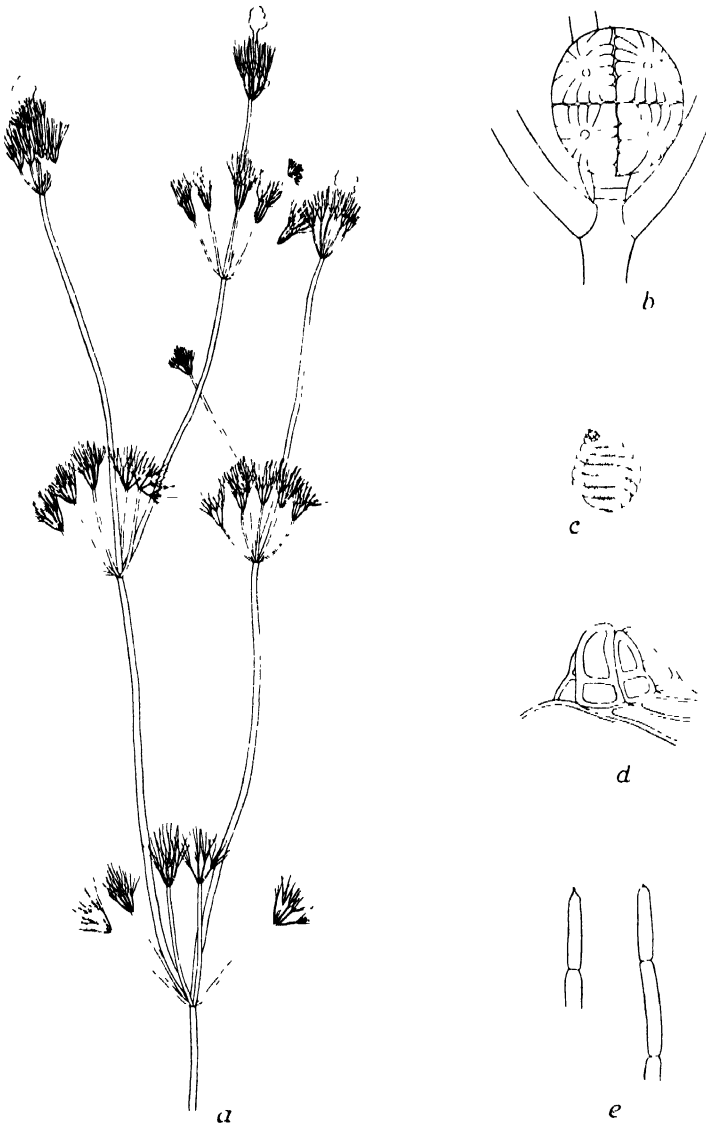
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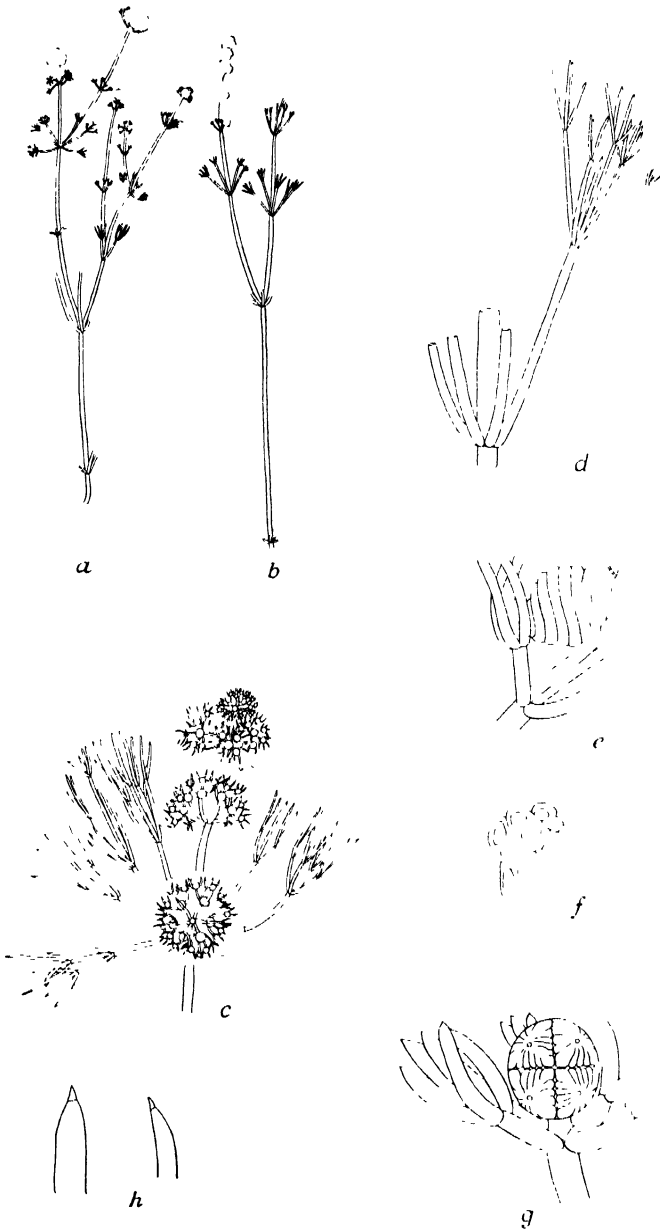
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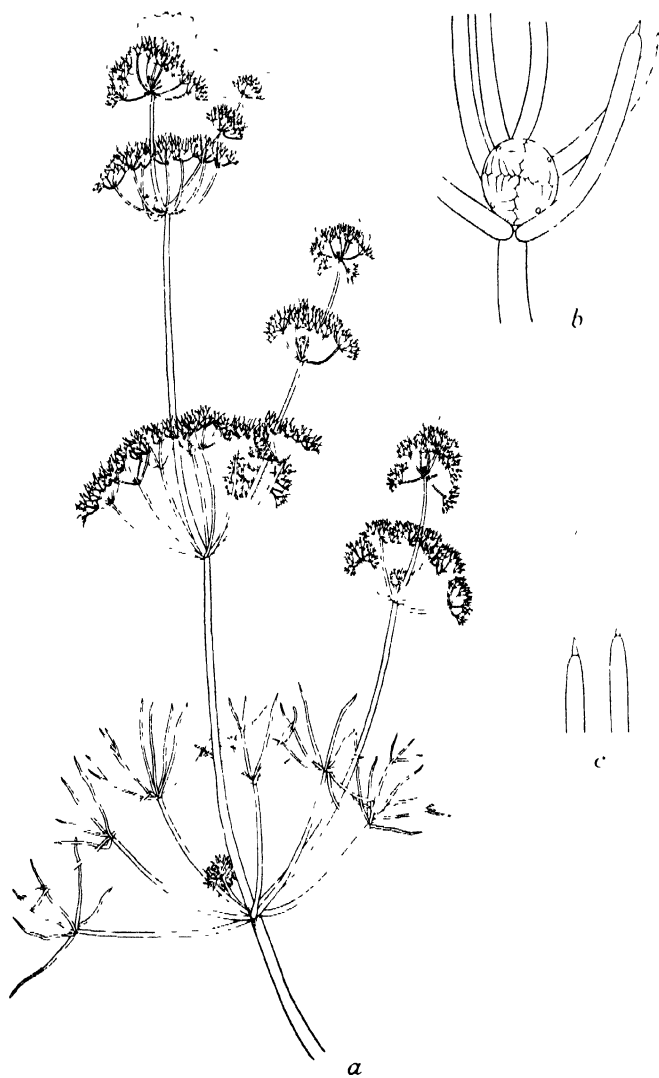
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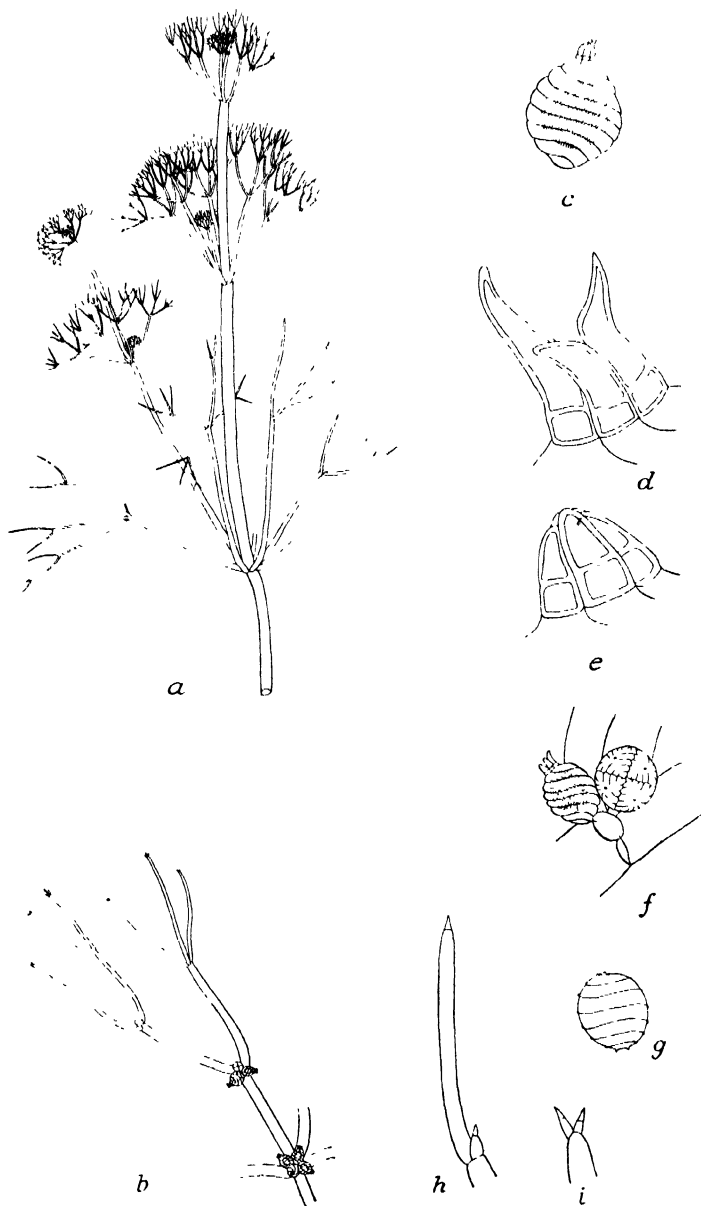
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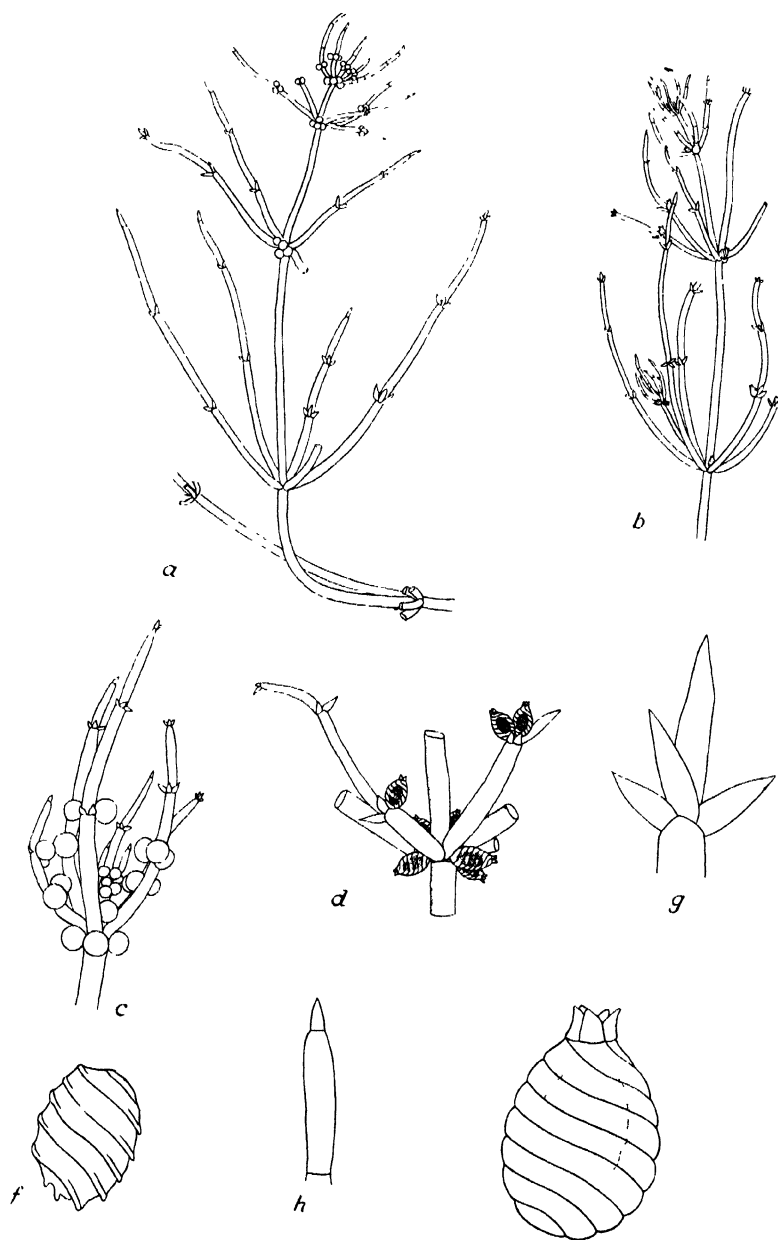
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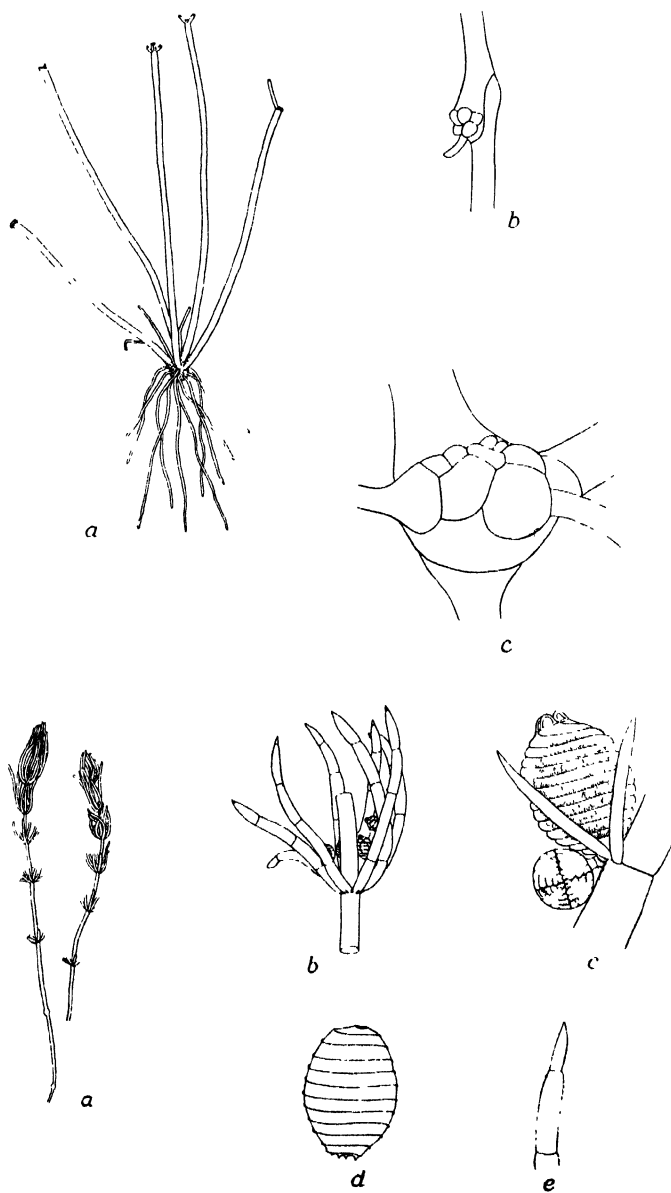
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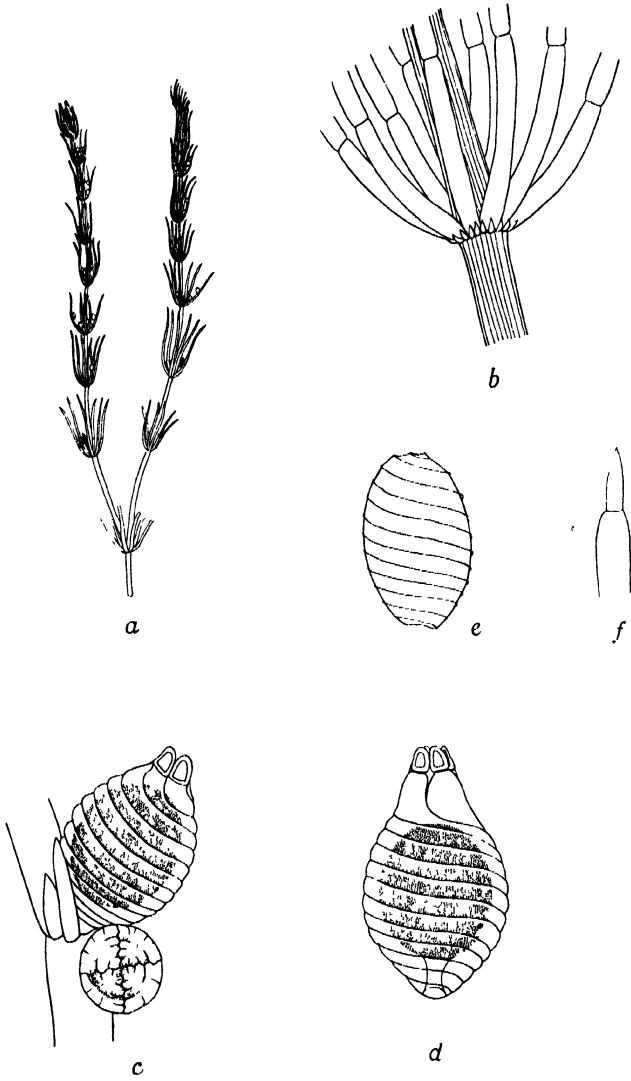
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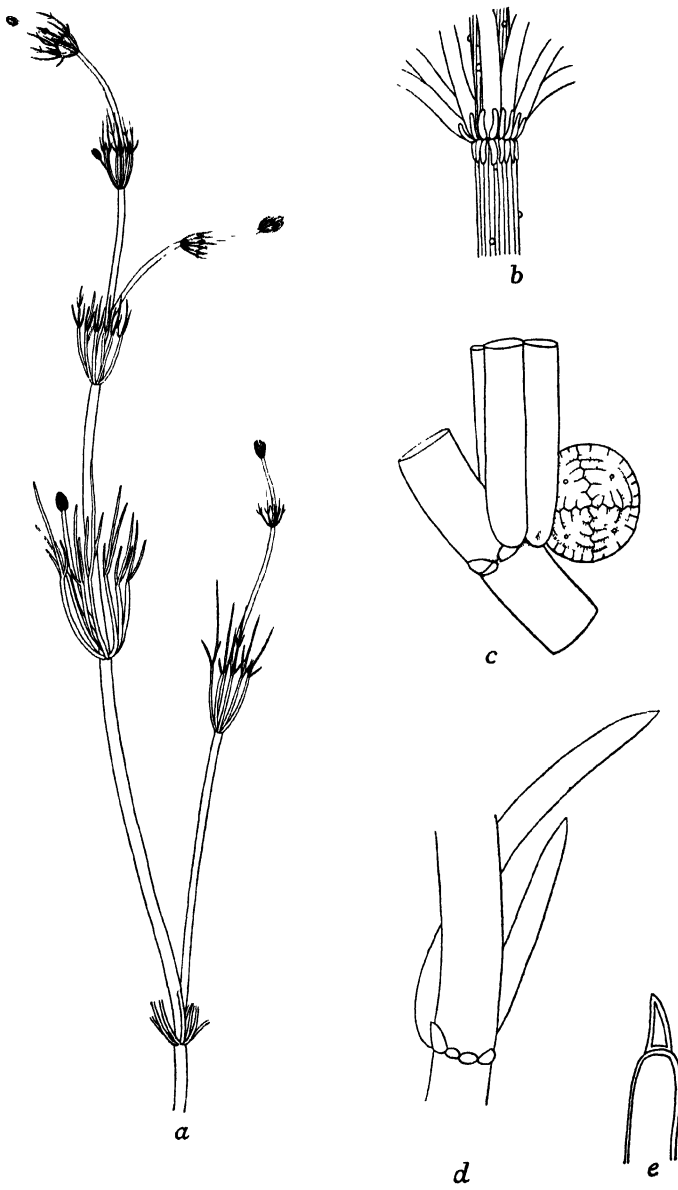
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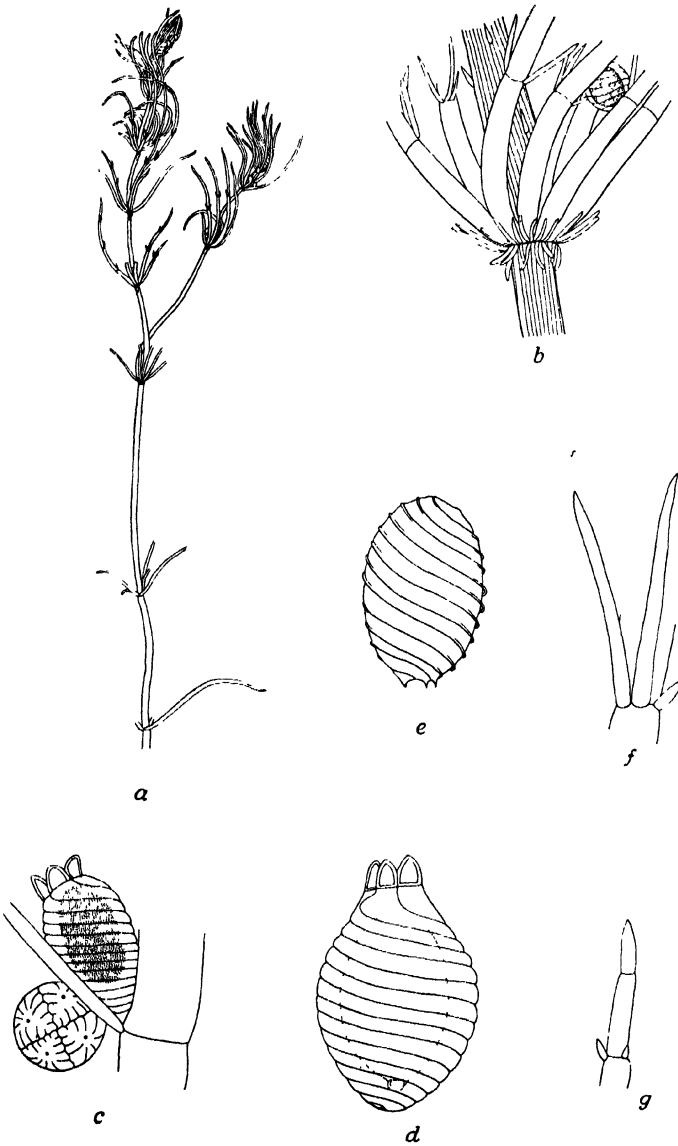
CHARA HANDAE sp. nov.

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EXPLANATION OF THE PLATES

PLATE 8.

N. superba, sp. n. (*a*) plant (nat. size), (*b*) antheridium, (*c*) young oogonium, (*d*) coronula, (*e*) apices of dactyls. (*b, c,* & *e,* × 30; *d,* × 240.)

PLATE 9.

N. globulifera, sp. n. (*a*) male plant (nat. size), (*b*) female plant (nat. size), (*c*) upper portion of male plant, (*d*) sterile branchlet, (*e*) oogonium, (*f*) coronula, (*g*) antheridium, (*h*) apices of dactyls. (*c* & *d,* × 7; *e, g,* & *h,* × 30; *f,* × 240.)

PLATE 10.

N. Annandalei, sp. n. (*a*) plant (nat. size), (*b*) antheridium, (*c*) apices of dactyls. (*b* & *c,* × 20.)

PLATE 11.

N. elegans, sp. n. (*a*) plant (nat. size), (*b*) fertile whorl, (*c*) oogonium, (*d*) antheridium, (*e*) coronula, (*f*) oospore, (*g*) ultimate node with dactyls, (*h*) apex of a dactyl. (*b,* × 7; *e* & *h,* × 240; all others, × 30.)

PLATE 12.

N. burmanica, sp. n.   (a) plant (nat. size), (b) part of branchlet, (c) oogonium, (d) coronula, (e) oospore, (f) dactyls.   (b, × 7 ; d, × 240 ; all others, × 30.)

PLATE 13.

N. polycarpa, sp. n.   (a) plant (nat. size), (b) part of branchlet, (c) oogonium, (d), (e) types of coronula, (f) fertile node, (g) oospore , (h), (i) dactyls.   (b, × 7 ; d & e, × 240 ; all others, × 30.)

PLATE 14.

C. Wallichii Braun.   (a) male plant (× ⅓ nat. size), (b) female plant (× ¼ nat. size), (c) branchlets with antheridia, (d) branchlets with oogonia, (e) oogonium, (f) oospore, (g) apex of branchlet.   (c & d, × 7 ; f & g, × 30.)

PLATE 15.

C. Wallichii Braun (*cont.*).   (a) basal portion of plant showing rhizoids (× ⅓), (b) rhizoidal node, (c) enlarged stem-node forming bulbil-like structure.   (b & c, × 30.)

C. nuda, sp. n.   (a) plant (nat. size), (b) fruiting whorl, (c) fertile node, (d) oospore, (e) apex of branchlet.   (b, × 7 ; all others, × 30.)

PLATE 16.

C. burmanica, sp. n.   (a) plant (nat. size), (b) portion of stem showing stipulodes, cortex, and bases of branchlets, (c) fertile node, (d) oogonium, (e) oospore, (f) apex of branchlet.   (b, × 13 ; all others, × 30.)

PLATE 17.

C. Grovesii, sp. n.   (a) plant (nat. size), (b) portion of stem showing stipulodes, cortex, spine-cells, and bases of branchlets, (c) fertile node, (d) sterile node, (e) apex of branchlet.   (b, × 13 ; all others, × 30.)

PLATE 18.

C. Handae, sp. n.   (a) plant (nat. size.), (b) portion of stem showing stipulodes, cortex, spine-cells, and bases of branchlets, (c) fertile node, (d) oogonium, (e) oospore, (f) sterile node, (g) apex of branchlet.   (b, × 13 ; all others, × 30.)

Further Notes on the Genera *Fumaria* and *Rupicapnos*.—II.
By H. W. PUGSLEY, B.A., F.L.S.

(PLATE 19)

[Read 4 February 1932]

IN 1919 a Revision of the genera *Fumaria* and *Rupicapnos* was published in the Journal of this Society, and this was followed in 1927 by supplementary notes, bringing together such further information on the group as had accumulated up to that date and describing several new species. Since 1927 much more has been brought to light concerning these plants. The French exploration of Morocco has extended, and Fumitories have been collected there, not only by Dr. Maire, but by M. Faure of Oran, by M. L. Emberger of the Institut Scientifique Chérifien at Rabat, and by M. Emile Jahandiez. Northern Morocco, formerly in the hands of the Riffs and now occupied by Spain, has also been visited by Dr. Font-Quer, of Barcelona, as well as by Dr. Maire ; and two interesting Fumarias have been collected by Dame Alice and the Misses Godman on a journey between Tangier, Rabat, and Marrakech.

As a result of this work in Morocco, three additional species of *Fumaria* and two of *Rupicapnos*, with some new varieties, have been discovered and are now described, as well as a very remarkable *Fumaria* found by Dr. Maire in the Kabylie district of Northern Algeria. A few new varieties from other countries are also included.

A brief account of the known natural habitats of *Fumariae* was given in the Revision, and additional details respecting the stations of the North African species were furnished in the Further Notes. The new forms from Morocco now to be described appear all to have been collected on rocks or other undisturbed ground, and it has become evident that in that country Fumitories are very frequently truly wild plants growing in natural stations. This is sometimes the case also in south-east Europe. In the spring of 1930, during a visit to Dalmatia, I had the pleasure of seeing *in situ* most of the species recorded for the Balkan Peninsula, and on the island of Lesina, where I spent nearly a week, *F. judaica*, *F. Petteri*, and more rarely *F. Kralikii*, were found growing as obvious natives on the bare stony screes of the coast-cliffs. It was noteworthy that *F. parviflora* could be seen only in the cultivated enclosures of the island. *F. judaica* was reported in 1915 by Dr. A. Ginzberger as occurring on some of the outer Dalmatian islets, which are bare rocks that have never been inhabited.

The sequence and method adopted in this paper follow those of the Revision and previous Supplement, unless stated otherwise, and the fresh descriptions, with italicised chief contrasting characters, have been similarly drawn up.

FUMARIA.

Sectio I. GRANDIFLORA.

Subsectio I. AGRARIAE.

The diagnosis of this subsection should be expanded to cover the anomalous species, *F. Mairei*, thus :—

. . . . . Fructûs . . . . . tuberculato-rugosi (*F. Mairei exceptâ*).

* Series Eu-Agrariae.

The diagnosis of this series now requires emendation, thus :—

Fructûs . . . . . rostrati (*nisi in F. agrariâ* var. *erostratâ*) . . . . .

1. FUMARIA AGRARIA Lagasca.

While most North African material of this species shows narrow, lanceolate sepals, approaching in form those of var. *mauritanica* Haussk., in the set ' Jahandiez, Pl. Marocc. 1923, no. 1 bis, Rabat,' as represented in Herb. Mus. Brit., the sepals are broadly ovate. The specimen recalls *F. atlantica* Coss. & Dur. by its habit and general appearance, but is shown by its fruit to belong to *F. agraria*.

A remarkable form has recently been sent by Dr. Maire, collected in four different localities in the Sous and Anti-Atlas districts of south-west Morocco. The specimens, which vary in size and form of the sepals, as so often happens in the case of *F. agraria*, are all notable for the form of their fruits, which are entirely beakless, although very strongly keeled and clearly a modification of those of ordinary *F. agraria*. The plant is distinguishable as a variety thus :—

δ. *erostrata*, var. nov.

Exsicc. Maire, Iter Marocc. xxi, Dar Lahoussin, Anti-Atlas, 1931 ! (Typus in Hb. Pugsley) ; Ait Baha prope Sidi Daoud, 1931 ! ; Taroudant, 1931 ! ; Ksima, in planitie Sous, 1931 !

Planta robustissima, laxa, petiolis cirrhosis scandens. Racemi laxi, multiflori (ad 40-flori), cum pedunculo ad 18 cm. longi. Sepala 2·5–4 mm. longa, ovato-lanceolata vel lanceolata. *Fructûs* 2·25–2·75 mm. longi, 2·75–3 mm. lati, *subrotundo-quadrati*, *subtruncati* (juniores breviter mucronati), *sine rostro conspicue carinati* vel fere subalati. Aliter ut in typo.

1 a. FUMARIA MULTIFLORA, sp. nov.   (Pl. 19, fig. 1.)

Exsicc. Dame Alice and the Misses Godman, Fl. Morocco, 1931, no. 119, Rabat–Casablanca–Marrakech ! (Typus in Hb. Mus. Brit.).

Fumaria *habitu laxo* sed *robusto*. Folia viridia, foliolis in exemplare viso in lobos planos satis angustos oblongos acutos vel mucronatos fissis irregulariter 2–3-pinnatisecta. *Racemi laxiusculi*, tandem longi, *multiflori* (–40-flori), *pedunculos* breviusculos *longe superantes*. Bracteae lineari-subulatae, acuminatae, *pedicellis* fructiferis 5–6 mm. longis *suberectis gracilibus* apice vix incrassatis

subduplo breviores. Sepala 3–3·5 *mm. longa,* 1–2 *mm. lata, lanceolata,* longe et tenuiter acuminata, parce irregulariter *laciniato-dentata,* nervo dorsali angusto albida plus minusve roseo-tincta, corollae tubo angustiora, in fructu nonnunquam persistentia. *Corolla magna,* 12–14 *mm. longa, roseo-albida,* ei *F. agrariae* subsimilis sed angustior ; *petalo superiore obtuso,* inferne satis angusto, *alis albidis* latis sursum reflexis carinam superantibus apicemque attingentibus praedito, calcare conspicue longicollo deflexo ; *petalo inferiore* obtuso *marginibus latiusculis patulis* apicem attingentibus subspathulato ; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs mediocres,* circa 2·5 mm. longi, 2 mm. lati, *ovati,* apice paulo attenuati, *acutiusculi, styli basi subapiculati,* inferne in stipitem angustum abrupte angustati, carinati sed parum compressi, siccitate apicis foveolis latis paulo obscuris *dense* sed tenuiter *rugosi.*

Haec pulchra *Fumaria F. agrariae* valde affinis est, sed per flores minores angustiores sepalis minoribus minus carinatis praeditos et per fructûs ovatos multo minores, tenuius rugosos, acutiusculos nec rostratos emarginatos differt. *F. rupestris* Boiss. & Reut. sepalis multo majoribus, corollis minus alatis etiam angustioribus, et fructibus vix ovatis magis compressis separanda est. *F. Ballii* Pugsl. per folia segmentis minimis magis decomposita, per sepala etiam minora, et per fructûs subrotundos nec ovatos plane diversa est. *F. atlantica* Coss. & Dur. propter flores majores latiores et fructûs maximos mucronatos facile distinguitur.

This fine fumitory, which seems to have been collected on a journey from Rabat southwards to Casablanca and Marrakech, is stated to grow in masses in its habitat, and it has perhaps been previously confused with *F. agraria.* It has not been possible to ascertain its exact station. The specimen on which the new species is founded is remarkably floriferous, one of its racemes bearing as many as forty flowers. Although it is obviously part of a vigorous plant, its foliage shows relatively small and narrow segments, but this may well be only an individual peculiarity, such as may sometimes be seen in allied species. The leaf-cutting appears quite different from that of *F. Ballii.* It is to be hoped that further material of this new plant will shortly be collected.

4. FUMARIA RUPESTRIS Boissier & Reuter.

A recent specimen at Kew, collected at Jaen in Andalusia (Ellman & Sandwith, no. 833 !), has good flowers and is not the variety *laxa* which grows at Ronda, but the typical North African *F. rupestris.* A second gathering of the same collectors from the vicinity (no. 793) probably also belongs to the specific type, although its flowers are too poor for certain determination. This is the first known evidence of the presence of typical *F. rupestris* in Spain. The species is now known to extend as far north as Toledo, in New Castile (Wilmott, rocky slopes near Alcantara bridge, 1926, in Hb. Mus. Brit. !).

A large robust form of this plant, collected at Ifrane, in the Middle Atlas,

has recently been received from M. L. Emberger, of the Institut Scientifique at Rabat. It possesses less narrow flowers than does typical *F. rupestris*, and larger fruits with black apical pits. It closely resembles the Spanish variety *laxa*, and may be identical with it, but better flowers, gathered earlier, are desirable.

Two specimens of a curious form, apparently growing in rock-clefts, and at first sight recalling a *Rupicapnos* in habit, have been forwarded by M. A. Faure, of Oran. These plants, which came from the Beni-Snassen region of Eastern Morocco, no doubt owe their form and peculiar foliage to nibbling by goats or other browsing animals, but their fruits are so characteristic that they seem worthy of varietal distinction, thus :—

δ. *platycarpa*, var. nov.

Exsicc. Faure, Martimprez-du-Kiss, au Guerbouz, 1930 ! (typus), et à Aghbal, 1930 ! in Hb. Pugsley.

Planta humilis, valde ramosa, haud elongata. Folia plerumque petiolata. *Racemi densiusculi*, 6–12-flori, *brevissime pedunculati*. Bracteae pedicellos circa 3 mm. longos subaequantes vel superantes. Flores in exemplaribus visis semi-depauperati sed verisimiliter ut in formâ typicâ. *Fructûs magni*, 2·75–3 mm. longi, 2·5–2·75 mm. lati, *subrotundo-quadrati*, obtusissimi, obsolete rostrati, valde carinati. Aliter ut in typo.

4 *b*. FUMARIA EMBERGERI, sp. nov.   (Pl. 19, fig. 2.)

Exsicc. L. Emberger, Chellah, près Rabat, 2.5.1931 !   (Typus in Hb. Instit. Scient. Chérifien et in Hb. Pugsley (no. 308)).

Fumaria verisimiliter *habitu laxo gracilique* petiolis cirrhosis scandens (an semper ?). Folia viridia, foliolis longe petiolatis in lobos, lanceolatos, plus minusve acutos, plane mucronatos fissis 2–3-pinnatisecta. *Racemi laxi*, sub-20-flori, *pedunculos* mediocres *subaequantes* vel primarii paulo longiores. *Bracteae* anguste lineari-oblongae, acutae, *pedicellis* fructiferis 5 mm. longis, gracilibus, apice paululum incrassatis, *erecto-patentibus plus duplo breviores*. *Sepala minima*, 1·5–2 mm. *longa, circa* ·5 mm. *lata, lineari-lanceolata*, acuminata, *subintegra* vel parce dentata, nervo dorsali viridiusculo albida, corollae tubo angusto angustiora, in fructu diu persistentia. *Corolla magna, angusta*, 12–14 mm. *longa, roseo-albida* ; *petalo superiore obtusiusculo, alis albidis* sursum reflexis carinam (in floribus bene explicatis) superantibus apicemque vix attingentibus praedito, calcare longiusculo paulum deflexo ; *petalo inferiore obtusiusculo marginibus latiusculis patentibus* ; petalis interioribus apice sursum curvatis breviter atropurpureis. *Fructûs modici*, circa 2·5 mm. longi, 2·25–2·5 mm. lati, *subrotundo-obovati, obtusi, breviuscule rostrati* (juniores acutiores longius rostrati), valde carinati sed parum compressi, inferne multo angustati, in sicco vix bifoveolati, *dense tuberculato-rugosi*.

Haec species nova *F. rupestri* (praesertim varietati *pallescenti*) proxima est, sed propter pedicellos longiores brevius bracteatos, sepala minima, petala

exteriora magis alata et fructûs acutiores specifice differre videtur. *F. multi-flora* per racemos multifloros, per sepala majora et per fructûs ovatos laeviores separanda est. *F. agraria* habitu multo robustiore, floribus majoribus lati-oribus, fructibus majoribus emarginatis longe distat.

F. Embergeri in dumetis apud Chellah prope Rabat in Mauritaniâ occidentali crescit.

This plant, discovered by M. L. Emberger, of the Institut Scientifique at Rabat, is evidently closely allied to *F. rupestris*, and especially to the variety *pallescens*, but its long pedicels with different bracts, its larger and more broadly-winged flowers with remarkably small sepals, and its more distinctly beaked fruits seem to warrant its description as a separate species.

5. FUMARIA BALLII Pugsley.

This rare species has been found this year (1931) by Dr. Maire in the Djebilet Mts. to the north of Marrakech, and in the Anti-Atlas to the south-west.

** Series **Orientales.**

9. FUMARIA JUDAICA Boissier.

While in the island of Lesina I found a form of this species, with fruits but little larger than those of *F. amarysia* Boiss. & Heldr., and more strongly keeled than in the typical form, growing on the stony cliff east of the little port of Hvar. Near the old Spanish Fort above the port and in other neighbouring localities the large-flowered variety *insignis* Pugsl. occurred in similar situations.

11. FUMARIA MACROCARPA Parlatore.

This species is still frequent at Ploce, outside Ragusa, and extends south-wards for some distance in bushy places along the cliffs, usually as a more or less rampant form. Its wholly milk-white flowers (which tend to become pink in drying) are very distinct. It also grows in Cyprus (G. C. Druce, 1928 !).

*** Series **Anomalae.**

Fructûs laeves.

11 *a*. FUMARIA MAIREI, sp. nov. (Pl. **19**, fig. 3.)

Exsicc. Maire, Kabylie, 1930 ! (Typus in Hb. Alger and Hb. Pugsley (no. 295)).

Fumaria *habitu* verisimiliter *satis robusto*. Folia virentia, irregulariter 2–3-pinnatisecta, foliolis subflabellatis in lobos ovato-rotundos ad oblongos obtusos mucronatos ad subacutos fissis praedita. *Racemi* in exemplare viso *densi*, 12–20-flori, *pedunculis* longiusculis plane *breviores*. *Bracteae* lineari-oblongae, acuminatae, *pedicellos* fructiferos *arcuato-recurvos aequantes* vel subaequantes. *Sepala* 4–5·5 mm. *longa*, 2·5–4 mm. *lata, subrotundo-ovata* vel ovata, peltata, *acuta*, praeter basin plus minusve dentatam *subintegra*, nervo angusto viridiusculo carinata, albida. *Corolla speciosa*, 12–13 mm.

longa, alba ; petalo superiore obtuso, latiusculo, dorsum compresso, calcar curvatum breve (circa 3 mm. longum) versus sulcato, *alis atropurpureis* sursum reflexis carinam multo superantibus et apicem attingentibus praedito ; *petalo inferiore* (2–3 mm. lato) *marginibus latis patulis* apicem attingentibus sursum paulo dilatatis obtuso subspathulato ; petalis interioribus sursum curvatis apice atropurpureis latiuscule alatis. *Fructûs modici*, 2·25–2·5 mm. longi, 2·25 mm. lati, ambitu *rotundati, obtusi*, parum compressi, subcarinati, siccitate apicis foveolis distinctis *laeves*.

F. *Mairei* propter corollam obtusam late alatam breviter calcaratam ad Subsectionem *Agrariarum* plane pertinet, sed, mirabile dictu, *F. capreolatae* L. pedicellos arcuato-recurvos, sepala magna subintegra et fructûs laeves monstrat. Per flores magnos albos apice atropurpureos etiam *F. flabellatam* Gasp. refert, sed ab hac petalis exterioribus obtusis late alatis, calcare breve et fructibus rotundatis laevibus facile distinguitur.

Haec species in quercetis montium Akfadou Kabyliae (ad alt. 700–1400 m.) Algeriae borealis habitat.

This beautiful Fumitory, described from limited material collected near Yakouren in the spring of 1930 by Dr. Maire, seems to be an anomalous species combining a corolla of extreme Agrarian form with the habit, recurved pedicels, large subentire sepals, and smooth fruits of *F. capreolata*. Dr. Maire reports (Bull. Soc. Hist. Nat. de l'Afrique du Nord, xxii, 276) that he has refound it in 1931 in the forests between Yakouren and Tala-Kitan. The forests of the Kabylie are extensive and in many parts not easily accessible—which may well account for this conspicuous plant having been hitherto overlooked.

SUBSECTIO II. **CAPREOLATAE.**

* Series **Eu-Capreolatae.**

12. FUMARIA CAPREOLATA Linn.

There is a specimen of this plant in Herb. Oslo from southern Norway (Fridtz, no. 12537, Mandal !), where it is perhaps of recent introduction. Exsiccata have also been noted from Tunis (Herb. Haun.), Tripoli (Herb. Kew.), and Madeira (H. G. Carter, St. Antonio, 2000′ alt., 1928 !).

ε. *devoniensis* Pugsley.

This variety still grows (1931) in its *locus classicus* at Woolacombe, in North Devon.

θ. *platycalyx* (Pomel) Pugsley.

Excellent material of this variety was collected by M. Faure in 1930 on rocks at Aghbal, Martimprez-du-Kiss, in the Beni-Snassen district of Morocco. The flowers, which are almost as pale as in var. *albiflora*, are 10–11 mm. long, with sepals 6 mm. × 3 mm., nearly as large as those of typical *F. macrosepala* Boiss.

13. FUMARIA DUBIA Pugsley.

An abnormal form of this species, bearing few-flowered racemes, was found

by M. Faure in 1923 on the borders of the railway near Oued-Imbert, to the south of Oran. There is also an example from Hammam Rihra in Herb. Mus. Brit.

13 *a*. FUMARIA FLABELLATA Gasparrini.

The form of this species which grows near Ragusa (Pugsley no. 294) shows rather narrow leaf-segments and irregularly recurved fruiting pedicels, thus approaching the variety *adriatica* Pugsl. In other respects, however, it agrees with the form found in South Italy and Algeria.

F. flabellata is now known from Malta (Herb. Mus. Brit.), and also from Corsica (Reverchon, no. 53, Otta, 1885, as *F. capreolata*, partim, in Herb. Mus. Brit. !).

** Series **Macrosepalae.**

The diagnosis of this series requires the following addition to cover the species *F. praetermissa* :—

. . . . . fructûs rugosi (*vel sublaeves*).

15. FUMARIA MACROSEPALA Boissier.

F. megasepala Pau, in Mem. Real. Soc. Esp. Hist. Nat. xii, 275 (1924), which is founded on *F. macrosepala* Ball, Spicil. 315, is conspecific with *F. macrosepala* Boiss. This is shown by Ball's original specimen in Herb. Kew, and is confirmed by recent material kindly sent by Dr. Maire from the *locus classicus* at Beni Hozmar, near Tetuan.

Another Moroccan plant, ' Font-Quer, Iter Marocc. 1929, no. 171, *F. capreolata* L. v. *oscilans* Pau & F.-Q. In umbrosis Sidi Brahim (Mtigua),' which has lately been received in Herb. Mus. Brit., is likewise a form of *F. macrosepala* Boiss. Mtigua is in the western Riff country, where the species might be expected to occur.

15 *a*. FUMARIA BIFRONS, sp. nov. (Pl. **19**, fig. 4.)

Exsicc. Jahandiez, Pl. Marocc. 1929, no. 211, ut *F. macrosepala* ! (Typus in Hb. Mus. Brit.).

Fumaria *satis robusta*, nunc humilis valde ramosa nunc petiolis cirrhosis scandens. Folia 2–3-pinnatisecta, foliolis in lobos oblongos vel ellipticos, subacutos vel obtusos mucronatos fissis praedita. *Racemi* 10–20- (in plantis debilioribus 4–10-) *flori, laxiusculi, pedunculos mediocres subaequantes. Bracteae* lineari-oblongae, acuminatae, *pedicellis* fructiferis elongatis (5–6 mm. longis), *suberectis vel erecto-patentibus,* flexuosis, apice multo incrassatis saepissime *dimidio breviores. Sepala* 4–5 *mm. longa,* 2–2·5 *mm. lata, oblonga* vel oblongo-ovata, peltata, plus minusve acuta, praesertim basin versus et in margine inferiore *leviter dentata,* nervo dorsali lato viridiusculo albida, corollae tubo paululum latiora. *Corolla speciosa,* 12–14 *mm. longa, alba,* saepe apicem versus

tandem paulo purpurascens ; *petalo superiore alis atropurpureis* sursum reflexis carinam paulo superantibus apicemque attingentibus *subacuto ; petalo inferiore marginibus latiusculis subpatentibus* apicem fere attingentibus acuto ; petalis interioribus apice atropurpureis sursum curvatis.   *Fructus majusculi,* 2·5–3 mm. longi ac lati, *sabrotundo-quadrati, subtruncati* vix mucronulati (juniores mucro-nulati), inferne abrupte angustati, plane compressi et *valde carinati,* siccitate apicis foveolis paulo obscuris dense *rugosi.*

Haec *Fumaria* speciosa ad Seriem *Macrosepalarum* certa referenda est sed florum forma colorque atque foliorum segmenta latiora *F. flabellatam* Gasp. simulant.   *F. berbericae* Pugsl. verisimiliter proxima est, sed foliorum seg-mentis latioribus, pedicellis longioribus cum bracteis multo minoribus, floribus majoribus, fructibus subtruncatis valdius carinatis satis differt.   *F. macro-sepala* Boiss. per pedicellos breviores, sepala multo majora (nisi in varietate *obscurâ*) subintegra, corollas angustatas, fructûs subrotundos laeviores distin-guitur.   *F. flabellata* pedunculis longioribus, racemis relative densifloris, pedicellis arcuato-recurvis, fructibus fere ecarinatis minoribus separanda est.

In rupestribus calcareis Moulay Bou Chta, infra Djebel Amergou (600 m. alt.) in regione Ouergha Mauritaniae borealis crescit (Jahandiez, 1929).

This handsome Fumitory, in the ensemble of its characters, most nearly approaches *F. berberica,* but it may also be regarded as intermediate between *F. macrosepala* and *F. flabellata,* the habit, racemes, and fruit clearly recalling the former, while the flowers themselves resemble those of the latter.   The station where it was found lies to the north of Fez and west of Ouezzan, and falls within the range of *F. macrosepala,* which is now known to extend to the Great Atlas.   *F. flabellata* has not been recorded for Morocco or Western Algeria.

16 *a.* FUMARIA PRAETERMISSA Pugsley in Journ. Bot. lxvi. 298 (1928).

There are specimens at Kew of this rare plant, received from R. T. Lowe (as *F. muralis* Sond.), from (1) Lanzarote, (2) Graciosa, (3) Betencuria, Fuerte-ventura, 1859, and (4) Selvagem Grande, coll. C. C. de Noronha, 1863.   The species is thus more widely spread in the Canary Islands than was at first supposed, and its occurrence in the Selvages Islands is of particular interest. These islands are a small group belonging to Portugal, and are situated about a hundred miles north of the Canaries and about a hundred and fifty miles south of Madeira.   They are uninhabited except for periodical visits of the Portuguese to collect barilla.   In 1869, as I learn from Dr. Sprague, R. T. Lowe published a ' Florulae Salvagicae Tentamen,' based on material collected by Noronha and enumerating sixty-two species af Phanerogams.   Lowe notes that the affinities of the Flora, which contains one endemic species, are largely with the Canaries, and *Fumaria muralis* (sic) appears on page 8, where its long bracts are duly mentioned.

SUBSECTIO III. **MURALES.**

* Series **Sub-Agrariae.**

18. FUMARIA BICOLOR Sommier.

There is a specimen of this plant in Herb. Kew. from Corsica (Forsyth Major, Propriano, 1917, as *F. agraria* !), and this year (1931) it has been found at Valescure, near St. Raphael, on the Riviera, by Mr. A. H. Maude.

19. FUMARIA BASTARDII Boreau.

An example of this species from Malta is now in Herb. Mus. Brit. Another specimen there (Vicioso, Calatayud, 1 June, 1910, as *F. affinis*), which belongs to the variety *Gussonei* (Boiss.) Pugsl., is labelled ' in rupestribus montanis ' and thus seems to have been obtained from a natural habitat. No other such station is known for *F. Bastardii*.

There is an excellent specimen of var. *hibernica* Pugsl. in Herb. Kew. from Point Lonsdale, Victoria, Australia (Tilden, 1912), where the plant has no doubt been recently introduced.

F. Bastardii has also been noted from the Cyclades (Rechinger, Myconos, 1927 !) and from the Canaries (G. C. Druce, Tamaracate, 1929 !).

** Series **Eu-Murales.**

20. FUMARIA MUNBYI Boissier.

This fine Fumitory was refound in good condition by Dr. Maire in June 1929, at Ketama, in the Riffian Atlas of Eastern Morocco. The specimen seen possesses the foliage of f. *major* Haussk., but its flowers do not exceed 11 mm. in length, and its pedicels are unusually short (3–4 mm.). It appears also to have been collected in 1927 by Dr. Font-Quer in the same region (Iter Marocc. 1927, no. 215, as *F. Gussonei* !), and near the Riffian littoral (Iter Marocc. 1927, no. 216, as *F. Gussonei*, f. *altera* !), but the material of these two sets in Herb. Mus. Brit. is weak and not characteristic.

The exsiccata ' Font-Quer, Iter Marocc. 1927, no. 217, *F. Munbyi*, Beni Hadifa ' in Herb. Mus. Brit. is a shade-form of *F. capreolata* L.

F. Munbyi has also been sent from Oran, the *locus classicus*, by M. Faure, who collected it there in 1914 ; and from Sidi Chami (Faure, 1908 !).

21. FUMARIA MARTINII Clavaud.

The locality of Vicioso's later gathering of this plant at Calatayud appears on his labels as ' Fentes des rochers siluriens,' and is probably a natural habitat.

An additional Spanish station for this plant is Plasencia, Estremadura (Lacaita, 1923). In Brittany it has recently been collected in Morbihan (Wilmott, 1925) and at Rochebrunne (Rechinger, 1926).

21 a. FUMARIA OUEZZANENSIS Pugsley.

An example of this showy species from the *locus classicus* is now in Herb. Mus. Brit. (Jahandiez, Pl. Marocc. 1929, no. 126 !). This has bracts somewhat shorter than those of the type and rather larger fruits (about 2·5 mm. long and broad), which are rugulose rather than rugose. *F. ouezzanensis* was also found by Dame Alice Godman in 1931 between Tangier and Rabat (no. 268, in Herb. Mus. Brit. !).

F. ajmasiana Pau & Font-Quer (Font-Quer. Iter Marocc. 1928 !) from Xauen is conspecific with *F. ouezzanensis*, as pointed out in Cavanillesia, iii, p. 49 (1930), by Dr. Maire.

22. FUMARIA SEPIUM Boissier.

The unnamed specimen in Herb. Kew., collected by Miss Bainbridge in South Morocco and referred to at p. 266 of the Revision, is probably a large-flowered example of this species, perhaps referable to var. *gaditana* (Haussk.) Pugsl.

23. FUMARIA MURALIS Sonder.

The exsiccata ' Font-Quer, Iter Marocc. 1929, no. 169. *F. muralis* Sond., Ras Sidi-el-Ahbed, Bocoia ' seem to be correctly named, although the specimens show only poorly developed fruit. This is the first example of *F. muralis* seen from the North African mainland, but the species is recorded for Algeria by Haussknecht. The district Bocoia (Bouccoya) lies in the Riff country to the west of Athucemas.

Among recent additions in Herb. Mus. Brit. is a specimen of var. *Lowei* Pugsl. from Portugal (Daveau, Azambuja !). This variety has hitherto been seen only from the Atlantic Islands.

23 b. FUMARIA MURALIS subsp. **BORAEI** (Jord.) Pugsley.

This plant is well represented in Herb. Oslo and appears to be widely distributed in Southern Norway as far as the Hardanger district. The specimens seen all agree with the original type of Jordan and are remarkably uniform, thus affording a marked contrast to the polymorphic forms of this group found in Britain.

There are now two Portuguese specimens of the subspecies in Herb. Mus. Brit. (Oliveira, Coimbra !). Both seem to belong to the typical form, but fruit is unfortunately missing.

<center>* * * Series Sub-Latisepalae.</center>

To cover *F. Petteri* the diagnosis of the series should be expanded thus :—

. . . . fructûs minimi (*vel mediocres*) . . . . .

25. FUMARIA PETTERI Reichb.

While in Dalmatia I visited Spalato and the island of Lesina, which are the original stations for this rare and critical species. At Spalato I was unsuccessful in finding the plant, but I met with it in Lesina close to the little port of Hvar.

The specimens obtained (Pugsley no. 301) were in good flower and fruit, and showed well the peculiarly ovate-elongate and stipitate capsules which characterise this plant. In this feature they exactly matched the form collected by Pichler at Monte Marian, near Spalato, but in foliage they were not identical, the leaf-segments being appreciably narrower, and recalling *F. Thuretii* Boiss. How far the difference may be due to environment is not quite certain.

In natural habitats on the stony screes about Hvar other closely allied plants also occurred. which seemed to connect *F. Petteri* with the varieties *Heldreichii* and *deflexa* of *F. Thuretii*. These were usually robust forms, with fine linear-oblong leaf-segments, very floriferous racemes, and variable fruits sometimes intermediate in size and shape between those of *F. Petteri* and typical *F. Thuretii*.

A further form seen sparingly in a few spots in Lesina bore short dense racemes of distinctly smaller flowers on straight pedicels, and very small fruits ; and this clearly seemed referable to the variety *pikermiana* of *F. Thuretii*, which has already been recorded for the island.

After seeing the assemblage of forms *in situ*, with its transitions of foliage and fruit characters, and remembering that all the plants of this group produce very similar flowers, in form unlike those of any other species, I am disposed to consider that they cannot be regarded as constituting two distinct species, and that a more correct view is to treat *F. Thuretii* (with its varieties) as a subspecies of typical *F. Petteri* Reichb , as defined at page 290 of the Revision The subspecies, as a whole, is separable mainly by its smaller and differently shaped fruits, and also by its normally narrower leaf-segments and smaller flowers. Its relationship with *F. Petteri* may be compared with that existing between *F. muralis* and *F. Boraei*. Under this treatment the aggregate species, *F. Petteri*, must be placed in the Series *Sub-Latisepalae*.

27. FUMARIA REUTERI Boissier.

This rare Spanish species was discovered by Dr. Maire in 1927 on calcareous rocks below Aourirt (1000-1200 m. alt.), in the middle Atlas of Morocco.

SECTIO II. PARVIFLORA.

SUBSECTIO IV. **LATISEPALAE.**

29. FUMARIA KRALIKII Jordan.

This pretty species grows in Lesina, on the stony slopes about Hvar and Milna, often in company with *F. Thuretii*.

30. FUMARIA MICRANTHA Lagasca.

There are several specimens of this plant in Herb. Oslo from Christiania, Fredrikstadt, and elsewhere in southern Norway, where it is perhaps of recent introduction.

The variety *dubia* Pugsl. was collected in 1928, by M. Faure, at Berkane, in the Massif des Beni-Snassen, in Eastern Morocco ; and near Fez in 1930

(Trethewy, Pl. Marocc. no. 314 c, in Hb. Kew. !). In 1931 it was found by M. Faure near Oued-Imbert and near Sidi-Bel-Abbès, in the province of Oran.

In 1906 a single plant growing with *F. micrantha*, and apparently a cross between it and *F. agraria*, was found by Bucknall at Aranjuez, in New Castile. The specimen shows intermediate foliage, very shortly peduncled racemes, pedicels and bracts recalling *F. agraria*, and rosy-white flowers, somewhat of *agraria* form, about 7 mm. in length, with small oval sepals. No mature fruit was seen.

31. FUMARIA BRACTEOSA Pomel.

There is an example of this species in Herb. Kew. from Western Persia (Macmillan, 1927, no. 15, Musjid-i-Suliman !).

<div align="center">SUBSECTIO V. OFFICINALES.</div>

33. FUMARIA OFFICINALIS Linn.

This species extends northwards in Scandinavia, mostly as f. *scandens* Pugsl., to the Alten district in Finmark (70° N. lat.), whence there are luxuriant examples in Herb. Oslo. In Norway the form *scandens* produces racemes up to 20 cm. long, bearing as many as forty deeply coloured and often very erect flowers, which sometimes reach 9 mm. in length. The sepals are always very narrow in these specimens, 3-4 mm. long, lanceolate, acuminate, and coarsely serrate ; and both of the outer petals are relatively narrowly winged.

A rampant form of the variety *Wirtgenii* Haussk. grows in Southern Norway, where it produces long racemes (20-30-flowered) with slender pedicels (3-4 mm. long), sepals 2 mm. long, deeply coloured but rather narrowly winged corollas (6-7 mm. long), and small, rugulose, flat-topped fruits 2 mm. long and broad. This form is represented in Herb. Oslo from Bygdo (Störmer, 1924 !), and Akershus Amt, Asker (Fridtz, no. 12518 !). Other examples, e.g., Fridtz, no. 12517, Vester-Aker ! &c., closely resemble this form, but have more typically *officinalis*-like fruits. Fries's *F. officinalis* γ *tenuiflora* (Novit. Fl. Suec. 221 (1828)) was apparently a shade-form of a similar plant.

The varieties *minor* Koch and *elegans* Pugsl. are also represented in Southern Norway, but are perhaps only recent introductions.

In North Africa *F. officinalis* is not very common, but the material seen includes examples of the typical form from Oran (Faure, 1910 !) ; of var. *minor* Koch from Maison Carrée (Pugsley, 1922), Tiaret (Faure, 1928 !), Oran (Faure, 1931 !), Terny (Faure, 1930 !), and Beni-Snassen, E. Morocco (Faure, 1930 !) ; of var. *densiflora* Parl., the characteristic southern form of the species, from Oran (D'Alleizette, 1922 !), Sidi-Bel-Abbès (Faure, 1931 !), Bossuet (Faure, 1927 !), and Beni-Snassen (Faure, 1929 !). A form of var. *Wirtgenii* Haussk. with small, highly coloured flowers only 6 mm. long was collected in the Middle Atlas by Jahandiez (Pl. Marocc. 1923, no. 493, Daïet Achlef, as *F. officinalis* v. *densiflora* !).

An unusual form of var. *Wirtgenii*, with very short pedicels and completely rounded fruits, occurs in the French Dept. Côte d'Or (Desplantes, Flavigny, 1929 !). A specimen of var. *elegans* has been seen from Hungary (Herb. Rechinger).

A new variety from Dalmatia is :—

ζ. *ragusina*, var. nov.

Exsicc. Pugsley, no. 293. Inter Ragusam et Gravosam Dalmatiae, 1930 !

Varietas racemis brevibus (10-20-floris), bracteis lineari-oblongis pedicello subduplo brevioribus, *sepalis* circa 2 mm. longis, *subrotundo-ovatis*, basin versus laciniato-dentatis, *corollâ circa 9 mm. longâ*, petalo superiore apiculato inferiore vix subspathulato interioribus plane sursum curvatis praeditâ, et *fructibus truncatis apice nigro-maculatis* a typo differt.

This very distinct plant, which I found in small quantity near Ragusa, is notable for its broad sepals and comparatively large corolla, recalling the Section *Grandiflora* by the relatively slight apical dilation of the lower and the upward curve of the inner petals. These characters suggest its derivation from the crossing of *F. officinalis* with *F. Bastardii*, but neither of these plants was seen in its vicinity and its fruits uniformly exhibit a normal development.

36. FUMARIA MICROSTACHYS Kralik ex Haussknecht.

The Herb. Mus. Brit. now possesses an additional example of this rare and local Egyptian species (Meinertzhagen, Matrich Wadi, 1928 !). The locality is not far from Cairo, and considerably extends the plant's known range, all of the earlier specimens having been collected at Alexandria. The flowers in this fresh gathering are deep rather than pale rose-coloured, with the lower petal obscurely spathulate.

SUBSECTIO VI. **MICROSEPALAE.**

* Series **Ambiguae.**

38. FUMARIA AUSTRALIS Pugsley.

Four further gatherings of this plant have lately been received at Kew, of which one (Saundy & Hancock, no. 76, Mt. Elgon, 9,000–10,000' alt., Uganda, 1930 !) exactly matches the original specimens collected by Volkens on Kilimandjaro. This seems to be the normal state of the species. Two other exsiccata (Fries, no. 1508, Kenia orient., 1923, as *F. abyssinica* !, and Snowdon, no. 1626, Lake Banyoni, Uganda, 1929 !) are slenderer forms, with laxer racemes and narrower bracts, and appear to be shade-forms of *F. australis.* ' Bagshawe, no. 396, Ruchiga,' referred to at page 309 of the Revision, and ' Stoltz, no. 2503,' are similar plants. These shade-forms are not unlike similar states of *F. abyssinica* Hamm., although, when normal and well-grown, this and *F. australis* are widely different. More material, with fruit as well as flowers, is desirable to determine their status with certainty.

38 *a*. FUMARIA ALGERIENSIS Pugsley.

Specimens of this plant collected by M. Faure at Oued-Imbert and Les Trembles, in the province of Oran, have flowers distinctly more deeply rose-coloured than those of the original type from Timgad.

** Series **Eu-Microsepalae.**

40. FUMARIA SCHLEICHERI Soyer-Willemet.

γ. *caucasica*, var. nov.

Exsicc. A. R. Jalova, Pl. Caucasicae, Soskoleka, 1906, in Hb. Kew., ut *F. Schleicheri* ? !

Planta *racemis longis multifloris* (–35-floris), *pedicellis* fructiferis quam in typo conspicue brevioribus, 2–3 *mm. longis*, apice incrassatis, bracteâ cuspidatâ vel tricuspidatâ suffultis, corollis laete roseis, *fructibus* circa 2·25 mm. longis, vix 2 mm. latis, *obovatis*, superne rotundato-obtusis, apiculatis, inferne plane angustatis, conspicue rugosis. Aliter ut in typo.

Haec varietas, quae Soskolekam prope Ekaterinodar Caucasi occidentalis habitat, prope racemos longiores cum pedicellis relative brevibus, floribus pallidioribus fructibusque plane obovatis a *F. Schleicheri* typicâ differt. *F. microcarpa* Boiss. per pedicellos etiam breviores longius bracteatos, per flores minores et per fructûs minimos subrotundos separanda est.

This well-marked var ety, which is notable in a species that appears to be unusually uniform considering its wide distribution, occurs in the region that produces *F. microcarpa*, and is possibly related also to that species, of which more material is much to be desired.

δ. *decipiens*, var. nov.

Exsicc. Pugsley, no. 307, Val d'Isère, 1931 !

Varietas *pedicellis vix* 3 *mm. longis*, *fructibus* plane latioribus quam longis (1·75–2 mm. longis, 2–2·25 mm. latis), *subrotundo-quadratis, fere truncatis,* brevissime apiculatis, a typo differt.

This plant, which was found at Le Fornet, above Val d'Isère, in Savoy, in July 1931, is readily separable from the normal species by its shorter pedicels and broad, very obtuse fruits.

41. FUMARIA MICROCARPA Boissier ex Haussknecht.

The material of ' Brotherus, Pl. Caucasicae, no. 42, Carthalinia, 1881 ' (as *F. Vaillantii*) in Herb. Kew. differs from that in Herb. Mus. Brit. (no. 426 ?), and is *F. microcarpa* instead of *F. Schrammii* var. *orientalis*.

42. FUMARIA INDICA (Haussk.) Pugsley.

It is not yet certain how far this species extends beyond the confines of India. Of the exsiccata mentioned on page 314 of the Revision, Kotschy, no. 133, from Persia, and Regel's Turkestan gathering (which is also represented at

Kew) are clearly *F. indica*. But the specimens (1) Polak, Kaswin, 1882, (2) Krassnow, Fl. Iliensis, 1886, (3) Meyer, Pl. Mongol. no. 720, and (4) Duthie, no. 8568, Quetta, consist of young plants only which more probably belong to *F. Vaillantii*.

43. FUMARIA VAILLANTII Loiseleur.

Of the copious Swedish material of this species in Herb. Oslo a few sheets might be referred to var. *Chavinii* Rouy & Foucaud, but the majority appear intermediate between that variety and the ordinary form of the species. As they were all collected in one district (Upsala), all of them probably belong in reality to one form which is not quite typical, and illustrate the remarks of Hammar and Haussknecht that this variety shades into the typical species.

It is probable, judging from the material at Kew and in Herb. Mus. Brit., that var. *conferta* Haussk. is widely spread in Persia and Central Asia, but many of the specimens are either in bad condition or too young for accurate determination.

The variety *maroccana* Pugsl. has now been found also in the Great Atlas of Morocco (Jahandiez, Pl. Marocc. 1927, no. 332, Ait M'Hammed, as *F. Schrammii* !).

A specimen of *F. Vaillantii*, approaching the typical form, collected in 1925 at Bedeau, in the province of Oran, has been received from M. Faure. This is the first example of this species that has been seen from Algeria.

44. FUMARIA SCHRAMMII (Ascherson) Velenovsky.

β. *orientalis* Pugsley.

While some specimens of *F. Schrammii* from the French Alps (e.g., Reverchon, Briançon, Dauphiné, 1875 !, and Vaucluse, Basses-Alpes, 1876 ! both as *F. Vaillantii*) are fairly typical, there are others in Herb. Kew. (e.g., Borel, Gap, Dauphiné, 1865 ! Gap, Hautes-Alpes, 1868 ! and Serres, Dauphiné, 1871 ! all as *F. parviflora*) which are referable rather to the variety *orientalis*, though with flowers more deeply coloured than usual. This variety has hitherto been seen only from Asia, except for the Spanish specimens, sent out as *F. caespitosa* Loscos, dealt with on page 320 of the Revision.

γ. *Pugsleyana* Maire.

This variety has been collected by Dr. Maire in a third station in the Moyen Atlas (In lapidosis calcareis prope Immouzer, 1900 m., 1927 !).

δ. *iberica*, var. nov.

Exsicc. Wilmott, S.E. of Cortijo, Vibora, Sierra Nevada, 1926, in Hb. Mus. Brit. !

Planta *compacta*, valde ramosa. Bracteae lineari-oblongae, acuminatae, apicem versus vulgo denticulatae, *pedicellos crassiusculos brevissimos* (circa 1 mm. longos) aequantes vel superantes. Sepala minuta, circa ·5 mm. longa, irregulariter triangulari-lanceolata. *Corolla pallide lilacino-tincta*, petali

superioris alis erecto-patentibus pallide purpureis. *Fructûs* vix 2 mm. longi ac lati, *subrotundo-obovati*, cum apiculo distincto persistente obtusi, inferne parum angustati, in sicco *rugosi*. Aliter ut in typo.

Haec varietas per habitum compactum var. *orientalem* et var. *Pugsleyanam* refert, sed ab alterâ pedicellis brevioribus fructibusque minus obtusis ab alterâ floribus lilacinis nec albidis fructibusque minoribus distinguitur.

This variety was found in the Sierra Nevada in a seemingly natural habitat on a bare slope at the upper limit of cultivation.

46. FUMARIA PARVIFLORA Lamarck.

There are recent examples at Kew of the rare varieties *latisecta* Haussk. (Muschler, Rosetta, Egypt, 1906 !) and *indicoides* Pugsl. (Chick, no. 116, Shiraz, 1928 !).

The species, apparently var. *glauca* Clav., is now naturalised in the Argentine (Venturi, Balcogna, Prov. Catamarca, 1898, in Hb. Mus. Brit. !).

An additional variety that seems worthy of distinction is :—

ι. *lutea* Doumergue in ' Les Hauts Plateaux Oranais,' p. 23 (1896).

Exsicc. Faure, Bedeau, Prov. Oran, 1909 !

Varietas habitu humili, foliorum segmentis brevibus crassiusculis, racemis brevibus pauci- (sub-10-) floris, floribus parvis verisimiliter albidis paulo lutescentibus, sepalis minimis, *fructibus* quam in typo *majoribus* (circa 2·5 mm. longis latisque) *magis compressis valde carinatis* brevissime apiculatis. Aliter ut in typo.

The material received from M. Faure under this name and collected in the *locus classicus* is characterised by large, broad, and strongly compressed fruits, quite distinct from those of any other form of the species.

A specimen in Herb. Mus. Brit. (Preston, no. 51, Mikra Bay, Salonika, 1918 !) has the appearance of being a hybrid between *F. parviflora* and *F. Schrammii.* It is almost, if not entirely, sterile, with foliage resembling that of *F. parviflora*, but with slender pedicels and lilac-coloured flowers recalling *F. Schrammii.*

RUPICAPNOS.

SECTIO III. TRIPTERYX.

9. RUPICAPNOS COSSONII Pugsley.

A specimen received from M. Faure, collected in 1919 on the rocks of Djebel Béguirat, near Bedeau, in the province of Oran, seems referable to this species. It appears to differ from the Batna type in its short, dentate bracts and its somewhat larger flowers (about 6 mm. long).

SECTIO IV. CALLIANTHOS.

SUBSECTIO I. **PERENNES.**

* Series **Cerefoliae.**

M. Faure has recently sent specimens, collected in June 1931 at Tinissen, in the Beni-Snassen Massif, which seem to belong to an undescribed species of this group. The plants are of dwarf growth, with remarkably glaucous foliage and flowers apparently like those of *R. ochracea* Pomel. The fruits, however, are large and of a different shape. The flowers are unfortunately not satisfactory for determination owing to the late date of collecting, and it is to be hoped that M. Faure will be able to revisit the district earlier in the season.

14. RUPICAPNOS GRACILIFLORA Pomel.

The exsiccata 'Jahandiez, Pl. Marocc. 1925, no. 127, Haute Moulouya' (as *F. africana*) is represented in Herb. Mus. Brit. by a single young plant in flower only. It probably belongs to *R. graciliflora*, but this cannot be confirmed in the absence of fruits and more mature examples.

* * Series **Africanae.**

19 *a*. RUPICAPNOS FAUREI, sp. nov. (Pl. **19**, fig. 5.)

Exsicc. Faure, Taforalt, Massif des Beni-Snassen, 2.5.1930, ut *Rupicapnos* —— ! (Typus in Hb. Pugsley).

Rupicapnos verisimiliter perennis sed radix haud visa. Caudex *caulibus satis gracilibus* saepissime brevibus sed nonnunquam elongatis decumbentibus ramosus. *Folia* parva, plus minusve carnosa, 5–10 cm. longa (petiolo haud crasso incluso), longissime petiolata, *oblongo-deltoidea*, foliolis 1–2-paribus breviter petiolatis et segmentis secundariis in *lobos oblongos acutos* vel obovatos obtusiusculos irregulariter fissis 2-*pinnatisecta* ; primaria subtrifida, in lobos latiores divisa. *Racemi* corymbiformes, 10–18-*flori*, cum pedunculo vix crassiusculo ad 4 cm. longo *foliis paulo breviores*. *Bracteae* 1·5–2 mm. longae, *oblongae*, mucronatae ; *pedicelli fructiferi filiformes*, apice incrassati, *infimi ad 30 mm. longi. Sepala 3–3·5 mm. longa, circa 2 mm. lata, oblonga* vel ovata, peltata, acuminata, plus minusve *repando-dentata*, praeter nervum dorsalem conspicuum viridiusculum albida, *conspicue arcuato-recurvata*, patentia, interdum in fructu persistentia. *Corolla 12–14 mm. longa, gracilis*, carinis viridiusculis *albida* ; *petalo superiore* marginibus purpureo-tinctis apice vix dilatatis deflexis vel patulis *lineari-oblongo obtuso, calcare 4–4·5 mm. longo rotundato fere recto ; petalo inferiore* marginibus patentibus apice vix dilatatis *sublineari subacuto*, basi *gibboso-saccato ; petalis interioribus* apice sursum curvatis *modice alatis atropurpureis.* Stylus malleiformis. *Fructûs majusculi*, sine mucrone 2·25–2·5 (raro 3) mm. longi, 2–2·25 mm. lati, *obovati, obtusissimi, plane mucronati*, inferne in stipitem distinctum angustati, satis compressi et valde carinati, in sicco omnino *dense tuberculato-rugosi.*

Haec species, in *Africanarum* Serie plane includenda, propter habitum relative gracilem et sepala recurvata notabilis est.   *R. africana* (Lamk.) Pugsl., quae per foliorum formam subsimilis est, habitu multo robustiore, foliis majoribus, sepalis latioribus nec recurvatis, corollis vix gracilibus, fructibus majoribus longius mucronatis recedit.   Folia lobis latioribus deltoidea, sepala latiora, corollae haud graciles, fructûs majores valdius tuberculati in *R. decipiente* Pugsl. videndi sunt ; foliis magnis, sepalis subrotundo-ovatis, corollis magnis, fructibus majusculis subacutis valde compressis *R. speciosa* Pomel depingitur ; *R. Mairei* Pugsl. per folia crassa anguste oblonga breviter petiolata, sepala orbicularia et fructûs magnos plane diversa est.

R. Faurei rupes ad meridianum spectantes prope Taforalt in montibus Beni-Snassen Mauritaniae orientalis habitat, ubi a cl. M. Faure anno 1930 collecta est.

This elegant *Rupicapnos*, of which good material, although lacking the root-stock, has been received with other plants of the family from M. Faure, of Oran, has the aspect of a small and remarkably slender *R. africana*. Its leaf-cutting is very similar, but the flowers, though slenderer, are more obtuse, the fruit is smaller and differently shaped, and the spreading recurved sepals are unique, so far as is known, in the whole genus.   Its peculiar features appear to warrant specific distinction, and it has been named after its discoverer.

20 *a*. RUPICAPNOS RIFANA, sp. nov.   (Pl. **19**, fig. 6.)

Exsicc. Font-Quer, Iter Marocc. 1928, no. 119, Xauen, ut *F. africana* ! (Typus in Hb. Mus. Brit.).

Rupicapnos perennis, caudice ramoso crassiusculo et habitu relative humili (an semper ?). *Folia* plus minusve glauca, carnosa, raro plus 6 cm. longa (petiolo crasso incluso), longissime petiolata, *subdeltoidea, foliolis* 2-paribus *subsessilibus* vel brevissime petiolatis irregulariter subtrifidis et segmentis secundariis in *lobos oblongos* inaeqüales *subacutos* fissis 2-*pinnatisecta subquinata*. *Racemi* corymbiformes, relative *pauci-* (saepius sub-10-) *flori,* cum pedunculo crassiusculo (ad 15 mm. longo) *foliis subduplo breviores. Bracteae* circa 1·5 mm. longae, *ovatae*, breviter cuspidatae ; *pedicelli fructiferi graciles,* apice paulo incrassati, *infimi ad 30 mm. longi. Sepala* 2–2·5 *mm. longa*, 1·5– 2 *mm. lata, ovato-deltoidea*, vix peltata, acuta, *basin versus dentata*, nervo dorsali viridiusculo albida. *Corolla magna*, 13–15 *mm. longa*, haud gracilis, carinis viridibus *albida* plus minusve purpureo-tincta ; *petalo superiore* marginibus purpurascentibus, apice vix dilatatis, patentibus vel deflexis, *oblongo obtuso, calcare breviusculo* (circa 4 mm. longo) rotundato deflexo ; *petalo inferiore* marginibus subpatentibus apice paulo dilatatis *lineari-oblongo subacuto* ad basin *gibboso-saccato ; petalis interioribus* apice sursum curvatis *anguste alatis atropurpureis*. Stylus malleiformis. *Fructûs modici*, sine mucrone 2–2·5 mm. longi, circa 2 mm. lati, *subrotundo-obovati, mucrone longiusculo obtusissimi*, inferne satis angustati, parum compressi et leviter carinati, siccitate omnino *dense tuberculato-rugosi*.

Haec species, quae ad *Africanarum* Seriem plane pertinet, propter habitum humilem, cum foliolis subsessilibus, racemis paucifloris, floribus magnis, fructibusque modicis conjunctum distinguenda est.

R. africana planta elatior est atque foliola breviter petiolata, flores angustiores et fructûs multo majores valde mucronatos habet. In *R. decipiente* flores subsimiles sed folia majora foliolis longe petiolatis magis dissecta fructûsque multo majores sunt. *R. Mairei* foliis angustis breviter petiolatis, sepalis rotundatis, corollis angustis minoribus et fructibus magnis facile separatur. Habitus elatior, folia segmentis longis magna, racemi multiflori cum pedunculo satis longo, et fructûs oblongo-elliptici subacuti valde compressi *R. speciosam* distinguunt. *R. Faurei* habitu gracili, floribusque angustissimis longe distat.

R. rifana in fissuris rupium calcarearum supra Xauen (vel Chaouen) in Mauritaniâ septentrionali habitat (Font-Quer, 1928).

This new species seems to be an essentially dwarf plant, with remarkably compact foliage and large flowers closely resembling those of *R. decipiens*.

*** Series **Pomelianae.**

22. RUPICAPNOS ORANENSIS Pugsley.

Through the kindness of M. Faure I was able to examine living material of this plant in the spring of 1931. Its flowers are less coloured than might be supposed from dried specimens being nearly white with more or less purple tinting only towards the apex.

In a parcel of exsiccata lately received from M. Faure there are three gatherings of a *Rupicapnos* from rocks in the vicinity of Taforalt (Beni-Snassen), which is closely allied to *R. oranensis*.   There is adequate material for the determination of each of these gatherings— in one case six complete plants in flower and fruit, which well illustrate the limits of variation.   The smallest plant on this sheet, which shows excellent flowers, has leaves only 2 cm. long, including the petiole, and presumably grew in a dry crevice.   The largest produced leaves 15 cm. long, and was probably taken from a comparatively moist and shaded chink.   Similar variations of foliage may be noticed with *R. numidica* in the Gorge at Constantine.   In all three gatherings the leaf-cutting of this Taforalt plant resembles that of *R. oranensis*, but the foliage seems to be less fleshy, particularly in the dwarf examples.   The flowers of the specimens are essentially those of *R. oranensis*, with small ovate sepals, a large rounded spur, and the lower petal conspicuously saccate.   The fruits are somewhat variable in form, but never of large size.   A fragmentary earlier example of the same plant, collected on Beni-Snassen by M. Faure in 1928, and another from Berkane, to the westward, also obtained by M. Faure in the same year, have been received from Dr. Maire.   'Font-Quer, Iter Marocc. 1929, no. 172, Hasdra Djeba, Mtigua' (as *F. africana*), appears to be the same plant : and this was found in fissures of calcareous rocks on the littoral.

From the aggregate characters of these specimens it may be concluded that they all belong to one form, and are most closely connected with *R. oranensis*, which grows about Oran and other localities to the east of the Beni-Snassen range, and also along the coast westwards. This form is best distinguished by its more slender habit and smaller fruits, and on the whole seems separable from *R. oranensis* as a variety only, thus :—

β. *gracilis*, var. nov.

Exsicc. Faure, Taforalt, vers Zegzel, 1930, ut *Rupicapnos* ——! (Typus in Hb. Pugsley) ; Faure, Berkane, Mt. Yaril (600 m. alt.), 1928, ut *Rupicapnos* ——!

Planta minor, foliis minus carnosis (praesertim in exemplaribus nanis), cum petiolo saepius gracili 2-15 cm. longis, lobis acutioribus nonnunquam praeditis ; corollis paulo minoribus, 10-13 mm. longis ; *fructibus minoribus* (2·5-2·75 mm. longis, 2·25-2·5 mm. latis), saepius *obtusiusculis* potius quam obtusissimis, minus compressis, a typo differt.

SUBSECTIO II. ANNUAE.

24. RUPICAPNOS FRATERNA Pugsley.

Specimens of this plant have been received from M. Faure, collected on rocks at Djebel Yaril (700 m. alt.), near Berkane, in 1928. This is the first certain record of this annual species for Morocco.

This year (1931) M. Faure has discovered, in very small quantity, at Tinissen, in the Beni-Snassen Massif, what appears to be a third annual species of this Section. Its foliage resembles that of *R. gaetula* (Maire) Pugsl., but the flowers seen are only about 9 mm. long, very slender, with conspicuous lanceolate, deeply toothed sepals. The fruits are quite small. It is hoped that more material will soon be obtained on which to base a satisfactory description.

EXPLANATION OF PLATE 19.

Fig. 1. Leaflet of *Fumaria multiflora* Pugsley, with flower and fresh and dried fruits.
Fig. 2. Leaflet of *Fumaria Embergeri* Pugsley.   do.   do.
Fig. 3. Leaflet of *Fumaria Mairei* Pugsley,   do.   do.
Fig. 4. Leaflet of *Fumaria bifrons* Pugsley,   do.   do.
Fig. 5. Leaf of *Rupicapnos Faurei* Pugsley,   do.   do.
Fig. 6. Leaf of *Rupicapnos rifana* Pugsley,   do.   do.

Foliage all natural size ; flowers and fruits, × 2·5.

INDEX.

[A star (*) denotes a name here published for the first time.]

A study of the changes following the removal of subalpine forest in the vicinity
of Arthur's Pass, Southern Alps, New Zealand.   By L. COCKAYNE, C.M.G.,
Ph.D., F.R.S., F.L.S., and W. A. SLEDGE, B.Sc., Ph.D.   (Dept. of Botany,
University of Leeds.)

(PLATES 20 & 21)

[Read 22 October 1931]

I. INTRODUCTION

Studies of definite successions lie at the root of advance in dynamic synecology,
but usually the period of observation is too short for satisfactory conclusions
to be drawn, or even for sufficient details to be secured showing the progress
of successional changes.   In the study presented in this paper the above
objections are lessened considerably for the following reasons :—

(1) Analogous studies were made in the same neighbourhood by L. Cockayne
thirty-four years ago, and his results lie open for reference * : while, in addition,
the present state of the above vegetation is being rather intensively studied
by J. W. Calder.

(2) A fair amount of information is given in ' The Vegetation of New
Zealand ' † in a condensed form when dealing with the subalpine forest and
scrub succession.

(3) A paper has been prepared recently by L. Cockayne, G. Simpson, and
J. S. Thomson ‡ on indigenous-induced vegetation for the New Zealand Region
as a whole.

(4) The period during which the vegetation of the area in question has
developed is some twenty-four years, a time sufficiently long to have enabled
definite communities to arise, while in no few instances different stages in the
development of successions can be observed from the earliest beginnings on
actual bare ground, up to the establishment of distinct communities, such
irregularities in the plant-covering as a whole depending upon different habitat
conditions, partly edaphic, but partly in accordance with aspect.

The area studied lies in the upper part of the Bealey Valley at the base of one
of the peaks of the Mt. Temple–Hills Peak Range, the altitude being about
850 metres above sea-level.   The site of the new vegetation was originally
low subalpine forest, with *Nothofagus cliffortioides* as the sole tree—a class

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* L. Cockayne.   ' On the Burning and Reproduction of Subalpine Scrub and its associated
Plants, with special reference to Arthur's Pass District.'   Trans. N.Z. Inst. xxxi, pp. 398,
419 (1899).

† L. Cockayne.   ' Die Vegetation der Erde.—XIV. The Vegetation of New Zealand,'
edition 2.   Leipzig, 1928.

‡ Published in ' The Journal of the Linnean Society, Botany,' vol. xlix. no. 326 (1932).

of forest, but more luxuriant, extremely common on the eastern slopes of the Southern Alps, notwithstanding that the tree-covering of the western slopes is of a subtropical rain-forest character. The area under consideration was denuded of forest in 1906–1907 by the Department of Public Works, in order to define the line of the tunnel now for some years in operation, which passes through the Southern Alps with its eastern and western exits in the Bealey and Otira Valleys respectively. Though we lack definite information, it seems clear, judging from the stumps and charred logs, that the forest was cut and subsequently burned, though some may have been burnt standing (Pl. **20.** fig. 2). The area is roughly oblong, with an average width of about 80 metres and an area of about 2·75 hectares. The new vegetation thus covers a considerable area and so affords opportunity for extended study ; and although this was impossible in our case, due partly to lack of time and partly to the weather, which was extremely bad, with high bitterly cold winds and almost constant driving rain or snow, yet a fair idea was obtained of (*a*) the original vegetation (the area being still surrounded by undamaged forest), (*b*) the successional progress of events, and (*c*) details of the competition between important members of the vegetation. In fact, though much remains to be done, this paper comes into line with the work formerly carried out by L. Cockayne, together with the recent intensive study by Calder of regeneration over the whole Arthur's Pass area—a study which we hope may be prosecuted from year to year for a considerable period.

II. THE ECOLOGICAL CONDITIONS

The average yearly rainfall of the district is approximately 3,500 mm., and there is no dry season. The area is swept by frequent north-west winds and less frequent south-west winds, the former generally blowing with extreme violence for several days at a time, though it is less in evidence on the pass itself, which is hemmed in by the adjacent lofty mountains. The violent winds influence greatly the rate of growth of early settlers on bare ground, but this by degrees will be increased or hastened through the plants sheltering one another, though with increase in height the wind is more acutely felt. The wind is generally accompanied by heavy driving rain which persists for several days, with short spells of fine cloudless weather during the summer when the ground becomes quite dry on the surface. The south-west wind is far less frequent, but it also blows with great power, and is not infrequently accompanied by snow. Following the snow storms there are often one or two fine sunshiny days to be succeeded rapidly by fresh storms of wind and rain from the north-west. In winter, snow lies 60 cm. or more in depth for a week or two at a time, and the temperature may fall to about −15° C., though −11° C. is a more common minimum. Frosts and snow occur during every month of the year, and the changes from frosty to quite warm weather are very rapid.

The soil is more or less peaty on top, but the subsoil is a boulder clay. The surface is very uneven and stones lying on it are a frequent feature. The water-content of the soil ranges from that which is completely saturated about bogs and rills, to that which is fairly dry and well drained on stony mounds and hillocks.

III. THE ORIGINAL VEGETATION

It has already been mentioned that the new vegetation is surrounded by low subalpine *Nothofagus* forest. This consists of two portions, the uppermost ascending the northern slopes of the range for some distance, the other forming a narrow belt alongside the West Coast road, which separates it from the great forest mass filling the valley below and densely clothing the flanks of Mt. Rolleston to the south. These two pieces of forest differ considerably in their structure and composition owing to the upper portion being boggy in places, and the lower portion being drier and the trees rather taller.

THE UPPER FOREST.—The *Nothofagus* trees are about 6 metres high and 25 cm. in diameter, and distant one metre or more from one another. In its richest development there is a rather tall middle layer of shrubs which includes a fair number of species, the following being the most important :—*Podocarpus nivalis* of spreading habit, *Dacrydium Bidwillii*, *Phyllocladus alpinus*, sapling *Nothofagus cliffortioides*, *Aristotelia fruticosa*, *Nothopanax Colensoi* var. *montanum*, *N. simplex* (juvenile and adult), *Pseudopanax lineare*, *Griselinia littoralis*, *Archeria Traversii*, *Dracophyllum longifolium*, *Suttonia divaricata*, *Coprosma pseudocuneata*, *Olearia arborescens*, *Senecio elaeagnifolius*.

As usual there are many deep mats of mosses on the forest floor, but there is also a considerable percentage of bare humus averaging 15 cm. in depth. The ground as a whole is irregular, with many fallen trees and rotting logs. The number of seedlings is in relation to the amount of light which the forest floor receives, the seedlings themselves being principally those of the plants listed above. *Astelia Cockaynei* is everywhere conspicuous with its silvery strap-like tufted leaves, the filmy ferns are represented by mats of *Hymenophyllum villosum* and *H. multifidum*, and ground ferns by *Polystichum vestitum*, a semi-tree fern.

Apparently many parts of the forest are traversed by streams, and on the more or less permanent wet ground in their vicinity the following species are common :—*Polystichum vestitum*, *Danthonia Cunninghamii*, *Schoenus pauciflorus*, *Corysanthes triloba*, *Viola filicaulis*, *Angelica montana* (occasional), the straggling *Hebe vernicosa* var. *canterburiensis*, much *Ourisia lactea*, mats of *Coprosma ramulosa* and *Erechtites glabrescens*. Where more light enters are *Rubus subpauperatus* var. *coloratus* and *Gaultheria rupestris*. The following species are also mentioned in our notes, but their ecological position is generally not indicated therein :—*Blechnum pennamarina*, *Lycopodium*

scariosum, Phormium Colensoi, Enargea parviflora, and *Ranunculus hirtus.*
A certain amount of sapling forest was noted which had originated through
the falling of old trees during heavy gales. Its undergrowth was much as
stated for adult forest, but its members were fewer.

The above details, though interesting enough to a student of New Zealand
vegetation, are not of particular moment to plant-ecologists in general, but the
following distinct points should have a wider interest : (1) The forest is quite
low, this depending upon its position in regard to the frequent heavy gales
and *not* on its altitude. (2) It contains a considerable number of subalpine
shrubs able to grow in the open, which might well be expected as common
constituents of the new vegetation, but this is far from being so ; while *Cassinia
Vauvilliersii,* so common in the new vegetation, is apparently absent. (3) In one
place at least where the forest has fallen there has been no regeneration of
Nothofagus, but a shrubbery has arisen or that has persisted which was
originally a portion of the undergrowth.

THE LOWER FOREST.—The *Nothofagus* trees are about 9 metres high and
about 30 cm. in diameter. The roof is open, and in consequence the under-
growth is dense. The floor is irregular, and on it lie many trunks and branches
covered with moss and lichen. Unlike the upper forest, beech saplings form
a large proportion of the undergrowth, and such saplings frequently form a
distinct second tier with an average height of 3 metres. The lower under-
growth contains fewer species than that of the upper forest ; it is dense and
consists principally of *Coprosma pseudocuneata* (dominant), *Phyllocladus
alpinus* (young), *Nothofagus cliffortioides, Nothopanax Colensoi* var. *montanum,*
and *Coprosma parviflora.* The shrubs are sparsely branched with slender
stems, whilst older tree-trunks are much mossed and bear many foliaceous
lichens. The ground vegetation is usually closed ; there is much *Astelia
Cockaynei* (physiognomic), *Ourisia lactea* (especially in good illumination),
Blechnum procerum and *B. pennamarina,* and a form of *Luzula campestris.*
In some places trees have been cut down and the undergrowth then consists
of *Hymenophyllum villosum, Phormium Colensoi, Pittosporum divaricatum,
Nothopanax simplex, Suttonia divaricata, Coprosma ramulosa* (forming mats),
and *C. foetidissima.*

IV. THE NEW VEGETATION

GENERAL.—As already stated, a series of transitions can be seen from the
early settlers on bare ground up to the final establishment of definite communities
distinct from one another. Therefore we attempt not only to deal statically
with the plant-covering, but also to some extent dynamically, though we are
generally without exact information as to the extent to which the diversity
of edaphic habitats determines the different classes of scrub.

It will be seen further on that the scrub falls into communities dominated by different shrubs. Such diverse domination is a common feature of the scrub-communities of the Arthur's Pass area, where there are not only two or three dominants as in the locality dealt with in this paper, but quite a number, the principal of which are the following :—*Dacrydium biforme, D. Bidwillii, Phyllocladus alpinus, Hoheria glabrata, Dracophyllum Traversii, D. longifolium, Hebe subalpina, H. buxifolia* var. *paucibrachiata,* and various shrub composites, especially *Olearia arborescens, O. ilicifolia, O. nummularifolia* (but generally these species are mixed together), and *Cassinia Vauvilliersii.* There are also mixed shrublands not dominated by any one species.

In addition to shrubland, two other associations occur as temporary climaxes, viz., tall tussock grassland and bog.

HERB-FIELD.—Excluding bog-communities the whole of the new vegetation falls into Cockayne's definition of Shrub Herb-field *, though it consists of several minor communities. The one dealt with here is made up chiefly of herbaceous and semi-woody plants.

Beginning with the bare ground, this apparently was occupied at first by various herbaceous and semi-woody plants, especially species of *Celmisia, Phormium Colensoi, Ranunculus Lyallii, Anisotome Haastii, Angelica montana,* and *Ourisia macrocarpa* var. *calycina.* As time went on, competition having taken place between the early comers (many of which are not mentioned above), certain of them became firmly established, and as the community developed such plants formed large colonies, as for example those species of *Celmisia* with tall erect rosettes (Pl. 20. fig. 1), or it may be that *Ranunculus Lyallii* took precedence, thanks to its massive, fleshy rhizomes, from which pass off its great saucer-like peltate leaves raised on long petioles. A colony of this kind cutting off all light and so forbidding invasion, would thus remain a striking feature for many years. By degrees the species of this herb-field proper are reinforced by others, since for a considerable time bare ground remains, suitable for settlement. Pieces of this class of herb-field differ in their composition in different parts of the area, such differences depending upon the nature of the edaphic habitat, its aspect, the time of arrival of the occupants, the relative rate of growth of the plants, and the viability of their seeds. About sixty-five species belong to this herb-field proper, the dominants in different parts of the community being particularly species of *Celmisia,* both tall and mat-like, *Danthonia Raoulii* (Pl. 21. fig. 4) in one or other of its varieties, together with their hybrids, *Phormium Colensoi* and *Ranunculus Lyallii.* The following are other characteristic members of the community :—*Polystichum vestitum, Blechnum procerum, B. pennamarina, Hypolepis millefolium, Lycopodium scariosum, L. fastigiatum, Hierochloe redolens, H. Fraseri, H. Fraseri×redolens, Astelia Cockaynei, Caladenia Lyallii, Pimelia prostrata, Gaultheria depressa, G. rupestris, Pentachondra pumila, Cyathodes*

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* L. Cockayne. ' Vegetation of New Zealand,' loc. cit. p. 311.

empetrifolia, Coprosma ramulosa, Celmisia coriacea, C. Armstrongii (Pl. **20.** fig. 1), *C. spectabilis, C. petiolata, C. petiolata*×*spectabilis, C. discolor, C. intermedia, C. laricifolia, Craspedia minor, Craspedia* unnamed species aff. *C. major*, and *Helichrysum bellidioides.*

The herb-field, thus briefly described, is clearly only an early succession, though some of it, as already suggested, may persist for a considerable time. It must be emphasised that herb-field proper, notwithstanding L. Cockayne's earlier treatment, is probably extremely rare as a permanent indigenous community, and that wide areas possessing a truly primitive physiognomy are undoubtedly indigenous-induced. The herbaceous and semi-woody members of herb-field proper are strongly light-demanding, and to this is due, at any rate in large measure, the ephemeral nature of the community as compared with shrubland : the species of the latter being mostly more tolerant of shade as seedlings than are most herbaceous and semi-woody plants.

As time went on bare places in the herb-field proper were invaded by shrubs, which as their stature increased by degrees cut off the light from the more lowly ground species and herbaceous plants, so that these were suppressed, and herb-field proper was replaced first by shrub herb-field and later by shrubland. This is by no means a universal happening for the New Zealand subalpine belt in general, because, though shrubs may enter herb-field in abundance, they cannot form closed communities where frequent high winds prevent the shrubs becoming tall. In such cases shrub herb-field forms a climax formation. Apparently this is not so in the area under discussion, as everywhere herb-field proper can be seen in process of transformation into shrubland by way of shrub herb-field.

SHRUBLAND.—Transitions from herb-field to shrubland are greatly in evidence over most of the area, dominance of shrubland being still a long way off. The shrubland consists of two distinct classes, the one dominated by *Dracophyllum longifolium* and the other by *Cassinia Vauvilliersii*. There is also more or less of what we here refer to *Dracophyllum uniflorum*, whilst *Hebe subalpina, H. vernicosa* var. *canterburiensis,* and *Coprosma parviflora* are all more or less common. *Nothofagus cliffortioides,* however, is conspicuously rare throughout the whole area, and, despite its dominance in the adjoining forest, shows no sign as yet of reasserting itself amidst the new vegetation. In addition to the shrubs settling on bare ground, the mat species of *Celmisia* make excellent seed-beds, though the tall rosette *Celmisiae* and *Phormium* do not behave in this manner. As time goes on, the shrubs grow into one another and shrubland—quite open at first, but finally with shrubs touching—becomes established, one physiognomic class of which is dominated by *Dracophyllum longifolium* (Pl. **20.** figs. 1, 2), and another physiognomic class by *Cassinia Vauvilliersii* (Pl. **21.** fig. 3), the dominant member of each greatly outnumbering other associated shrubs. Frequently the *Dracophyllum* bushes have not killed out all the species beneath them, and as survivors

the following tolerators of a fair amount of shade may be cited :—*Blechnum procerum*, *B. pennamarina*, *Cyathodes empetrifolia*, and *Ourisia macrocarpa* var. *calycina*. Where adjacent shrubs do not touch, species of herb-field proper remain, including *Celmisia spectabilis* and *Gaultheria rupestris*. The *Dracophyllum longifolium* community is often almost pure. The bushes average about 1½ metres in height, and the community is readily recognisable at a distance by the brownish tint of the bush and the dense and grass-like foliage. With the *Dracophyllum* may be those shrubs mentioned above as invaders of herb-field proper, the species of *Hebe*, however, playing an insignificant part.

The *Cassinia* association (Pl. 21. fig. 3) has usually not reached the closed stage, nor are the bushes of the dominant fully developed. They are of spreading habit, averaging 60 cm. in height and twice as much in breadth. The ground beneath or in the immediate proximity of the *Cassinia* bushes is either bare or, more usually, is occupied by the following species :—juvenile *Dracophyllum longifolium*, *Celmisia Armstrongii*, *C. coriacea*, and *C. discolor*, together with very small *Blechnum pennamarina*, stunted *Lycopodium fastigiatum*, patches of *Danthonia setifolia*, *Luzula campestris*, *Phormium Colensoi*, *Epilobium tasmanicum*, large mats of *Pimelia prostata*, *Gaultheria rupestris*, and, on peaty ground, numerous mats of *Cyathodes empetrifolia*.

Bog.—Previous to the burning of the forest, the present bog would be represented by specially wet ground such as still occurs in the upper forest. *Sphagnum* is now conspicuous, and the close mats of the sedge *Carpha alpina* form a ground-work amongst which and elsewhere in the bog the following characteristic species occur :—*Dacrydium biforme*, *D. Bidwillii*, *D. laxifolium*, *D. Bidwillii* × *laxifolium*, *Oreobolus pectinatus*, *Schoenus pauciflorus*, *Drosera Arcturi*, *D. spathulata*, *Pentachondra pumila*, *Cyathodes empetrifolia*, *Ourisia lactea*, *Celmisia glandulosa*, *Craspedia minor*, *Gnaphalium paludosum*, *Senecio Lyallii*, *S. angustatus*, and certain species which are not specially denizens of bogs, e.g., *Celmisia intermedia*. There grow on the bog many tall tussocks of *Danthonia Raoulii* var. *flavescens* together with var. *rubra* and a swarm of hybrids between these two. This points clearly to the fact, well recognised elsewhere, that the bog at no very distant date will be transformed into tall tussock-grassland.

TALL TUSSOCK-GRASSLAND.—This can be seen in process of establishment in many places, its early beginning being were *Danthonia Raoulii* in its various forms dominates the incipient herb-field. On the moraine it is specially well developed, but it is hardly likely to become an outstanding feature of the area owing to the superabundance of shrubs, though doubtless areas will persist for a considerable time and even form a sub-climax community. Associated species are mainly those of herb-field proper, but in one place a good deal of *Hebe buxifolia* var. *paucibrachiata* was observed, a sign generally of wettish ground.

INDETERMINATE COMMUNITIES.—There is a good deal of old moraine on the area (Pl. 21. fig. 4), the chief ecological characters of which are the large number of rocks and stones of all sizes, frequent short steep faces, various depths of soil amongst the stones, and rapid drainage, this latter being a contrary character to that of the more level ground, though even there, despite the heavy rainfall, water generally does not lie for very long.   Evidently there are many different *growing places* for the plants, and, in consequence, the plant-covering will be far from uniform, and eventually consist of a close growth of different shrubs, several of which will be in fairly equal proportions.   At present, on the drier stony ground, there is a good deal of the mountain variety of *Gaultheria rupestris* distinguished by its thick obtuse leaves.

VEGETATION ON THE BANKS OF STREAMS.—A diverse plant-population characterises the banks of the small streams, and various shrubs grow luxuriantly here, e.g., *Nothopanax Colensoi* var. *montanum*, the species of *Hebe* and *Olearia* of the locality, and *Cassinia Vauvilliersii*.   These shrubs, rooted on both sides of the stream, frequently grow into one another.   The following herbaceous and semi-woody plants are common and luxuriant :—*Danthonia Raoulii* in its varieties *flavescens* and *rubra*, *D. Cunninghamii* (this hybridizes with *D. Raoulii*), *Schoenus pauciflorus*, *Phormium Colensoi*, *Anisotome Haastii*, *Angelica montana*, *Ourisia macrocarpa* var. *calycina*, species of *Celmisia* including those with tall rosettes, and *Senecio Lyallii*.

V. EXOTIC PLANTS IN THE AREA

The relation of the exotic and indigenous floras of New Zealand has always been of intense interest to biologists in general, and especially to students of evolution.   Quite early in the investigation of New Zealand natural history, thanks to the writings of Darwin, Wallace, and Travers, it became a matter of biological faith that when exotic plants invaded an area occupied by those indigenous to the soil, the latter went to the wall and the foreigners became supreme.   Later T. Kirk and T. F. Cheeseman assisted in spreading this doctrine.   It was not indeed until 1900 that L. Cockayne first showed the belief to be untrue, and since that date he and others have brought forward fact after fact which should, long ere this, have exploded the erroneous theory. Be this as it may, it seems to us a matter of considerable interest to point out what has happened in the area dealt with here, which twenty-four years ago was bare ground, ready for invasion by any plant-colonists, the seeds of which might alight thereon.   There were, of course, seeds of indigenous plants available from the open ground of Arthur's Pass, and also those of trees and shrubs from the adjoining forest.   But there were as well, at no greater distance away than two kilometres, at least fifty alien plants *, many of which are well-known weeds with high powers of dissemination.   In addition, seven were noted growing on the adjacent road-side, and also on that part of the

* See Appendix II.

Pass where from time to time cattle and sheep are grazed. It thus appears almost as if an ideal unpremeditated experiment had been set in train contrasting the relative aggressiveness of indigene and exotic, the former, however, with ecological conditions both edaphic and climatic, to which it had always been accustomed. Each high wind in due season would bring to the bare soil seeds in abundance of both classes of plants, so that should certain species not gain a footing it would seem as if they were unsuited to do so. Yet no less than ninety-three species of indigenous plants are more or less firmly established on the area, whilst the remarkable fact came to light that only two exotics, viz., *Hypochaeris radicata* and *Holcus lanatus*, have gained a footing, and in such small numbers (three or four of each) as to be negligible *. Soil-conditions may in part be responsible for this meagre representation, but these surely should not have hindered the wide spreading of the species mentioned together with *Rumex Acetosella* and several other members of the weed florula.

Even more remarkable is the almost entire absence of any species of the indigenous genus *Acaena* (only one small plant was seen close by the side of a track), notwithstanding their barbed fruits so suitable for distribution by animals. Nor had the species of *Acaena* far to come, since for years they have lined the roadside close to the area. Occasional animals, too, are not wanting for their dissemination, especially the dog, hare, sheep, and man. Yet, on the sheep-runs in the drier mountain areas of New Zealand, the species of *Acaena* have become such serious weeds as to induce the Government to combat the pest by the introduction of some natural insect enemy.

VI. SUMMARY OF RESULTS

(1) This paper deals with the new vegetation which has arisen after the burning of a piece of subalpine *Nothofagus cliffortioides* forest twenty-four years ago.

(2) The locality is in the upper Bealey Valley at an altitude of about 850 metres above sea-level, a little to the east of Arthur's Pass (Southern Alps of New Zealand), and separated therefrom by a small strip of subalpine forest.

(3) The area of new vegetation is about 2·75 hectares.

(4) The climatic conditions to which the plants are subjected are, in the main, extremely high winds, a high rainfall, frequent rainy days with sudden changes to cloudless sky, fairly deep snow in winter—but only for a week or two at a time,—and frost and snow in every month of the year.

(5) This new vegetation is surrounded on all sides by a continuous belt of the original forest, so that the old vegetation and the new can be conveniently contrasted.

* Probably a few others occurred, the time of year and snowy conditions very probably accounting for some having escaped our notice, but it is certain that both the number of exotic species and also the number of individuals is extremely small. By the adjacent road-side the following exotic plants were noted :—*Anthoxanthum odoratum, Agrostis alba, Holcus lanatus, Rumex Acetosella, Trifolium pratense, T. repens,* and *Hypochaeris radicata,*

(6) The forest is stunted owing to the frequent high winds which sweep through the Pass, with *Nothofagus cliffortioides* as the sole tree and an undergrowth of various shrubs, herbs, and semi-woody plants, many of which do not occur in the new vegetation.

(7) Owing to the diverse nature of the edaphic habitat, especially in regard to its suitability for the rapid growth of the invading plants, every stage can yet be observed from that of bare soil being invaded up to that of a sub-climax vegetation.

(8) At the present time the whole vegetation may be defined as shrub herb-field, which is a community having a large percentage of herbaceous and semi-woody plants, and mat-shrubs as a ground-work, out of which rise solitary shrubs or groups of shrubs to form distinct assemblages.

(9) Analysing the shrub herb-field, it consists of the following classes of vegetation :—Herb-field proper, *Dracophyllum* shrub-land, *Cassinia* shrub-land, bog, and a mixed vegetation of old moraines and stream-sides.

(10) *Nothofagus cliffortioides* is rare in the new vegetation, and gives no indication of future re-dominance.

(11) Notwithstanding the proximity of many aggressive exotic plants so few have entered the area as to be quite negligible. Also various species of the extremely aggressive indigenous *Acaena,* so readily distributed by means of their hooked seeds, are absent, although *Acaena* in profusion grows close to the area along the roadside where the forest-belt is absent.

(12) The vascular species number 93 and belong to 28 families and 53 genera. All are members of the adjacent plant-covering of Arthur's Pass and the forest-belt, but many belonging to these two areas are wanting.

VII. LIST OF THE VASCULAR SPECIES OF THE NEW VEGETATION

Abbreviations :—d. = dominant ; la = locally abundant; ld = locally dominant;
a. = abundant ; f. = frequent ; o. = occasional ; r. = rare ; l. = local.

[The relative frequency given in this table is an estimate and is not based on statistical observations.]

Species etc.	Community.	Remarks.
Agrostis Dyeri Petrie	Herb-field, o.	Allied to the northern *A. canina* L.
Angelica montana (J. R. & G. Forst.) Ckn.	Herb-field (stream-sides, wet places), la.	
Anisotome Haastii (F. Muell.) Ckn. & Laing.	Herb-field, f.	
A. pilifera (Hook. f.) Ckn. & Laing.	Herb-field, f.	
Asperula perpusilla Hook. f.	*Cassinia* shrub-land, r.	
Astelia Cockaynei Cheesem. .	Herb-field, a.	
Blechnum pennamarina (Poir.) Kuhn.	Herb-field, a. ; shrubland, a.	

Species etc.	Community.	Remarks.
B. procerum (Forst. f.) J. G. Anders.	Herb-field, f.; shrubland, f.	Probably a species distinct from the huge fronded lowland form of shady banks.
Caladenia Lyallii Hook. f. ..	Herb-field, r.	
Cardamine heterophylla (Forst. f.) O. E. Schulz.	Herb-field, o.	
Carpha alpina R. Br.	Bog, f.	
Cassinia Vauvilliersii (Homb. et Jacq.) Hook. f.	*Cassinia* shrubland, d.; *Dracophyllum* shrubland, o.; herbfield, a.; bog, r.	Well-grown shrubs average ⅔ m. in height.
Celmisia Armstrongii Petrie .	Herb-field, ld.; shrubland, o.	
C. coriacea (Forst. f.) Hook f.	Herb-field, ld.; shrubland, o.	
C. discolor Hook. f.	Herb-field, ld.; shrubland, o.	
C. glandulosa Hook. f.	Bog, f.	
C. intermedia Petrie	Herb-field, a.; bog, o.	
C. laricifolia Hook. f.	Herb-field, f.	
C. petiolata Hook. f.	Herb-field, ld.; shrubland, r.	
C. petiolata × spectabilis	Herb-field, o.	One of the forms of this is *C. mollis* Ckn.
C. spectabilis Hook. f.	Herb-field, ld.; *Dracophyllum* shrubland, o.	
Coprosma parviflora Hook. f.	Herb-field, f.; *Dracophyllum* shrubland, f.	
C. propinqua A. Cunn.	Herb-field, o.	
C. pseudocuneata W. R. B. Oliv.	Herb-field, f.	
C. ramulosa Petrie	Herb-field, f.	
C. serrulata Hook. f.	Herb-field, o.	
Cotula squalida Hook. f.	Herb-field (trackside), r.	
Craspedia minor (Hook. f.) Ckn.	Herb-field, o.; bog, f.	
C. sp. (aff. *C. major*)	Herb-field, o.	
Cyathodes empetrifolia Hook. f.	Herb-field, a.; shrubland, o.; bog, a.	
Dacrydium biforme (Hook.) Pilger.	Bog, o.	
D. Bidwillii Hook. f.	Bog, f.	Shoots more slender than in *D. biforme*; both have short spreading leaves in juvenile stage, which occurs along with adult stage.
D. Bidwillii × laxifolium	Bog, r.	
D. laxifolium Hook. f.	Bog, f.	

Species etc.	Community.	Remarks.
Danthonia Cunninghamii Hook. f.	Herb-field, a. Tussock-grass-land, o.	
Dianthonia Cunninghamii × either or both vars. of *D. Raoulii*.	Herb-field, f. Bog, o.	
D. Raoulii Steud. var. *flavescens* (Hook. f.).	Herb-field, a; Cassinia shrub-land, a; tussock grassland, a; bog, a.	Large group of many forms.
D. Raoulii Steud. var. *rubra* Ckn., ined.		
D. Raoulii var. *flavescens* × var. *rubra*.		
D. setifolia (Hook. f.) Ckn....	Herb-field, a; Cassinia shrub-land, o.	
Dracophyllum Kirkii Berggr.	Herb-field, r.	On moraine chiefly.
D. Kirkii × *longifolium*	Herb-field, r.	
D. longifolium (Forst. f.) R. Br.	Herb-field, a; *Dracophyllum* shrubland, d; *Cassinia* shrub-land, f.	Well-grown shrubs average 1·25 m. in height, but all stages from seed-lings to fully grown shrubs are present.
D. longifolium × *uniflorum* ..	Herb-field, r; *Dracophyllum*, shrubland, r.	One form of the hybrid group greatly resembles *D. acicularifolium* (Cheesem.) Ckn., to which it has been referred by W. R. B. Oliver.
D. uniflorum Hook. f.	Herb-field, f; *Dracophyllum* shrubland, f.	This may be *D. rosmarinifolium* (Forst. f.) R. Br. It is not identical with *D. uniflorum* of the drier mountains.
D. Traversii Hook. f.	Herb-field, r.; *Dracophyllum* shrubland, r.	So far only very young plants observed, one of which resembled *D. longi-folium* × *Traversii*.
Drosera Arcturi Hook.	Bog, f.	
D. spathulata Labill.	Bog, f.	
Epilobium chloraefolium Hausskn.	Herb-field, o.	
E. pedunculare A. Cunn.....	Herb-field, f.	
E. pedunculare var. *brunnescens* Ckn.	Herb-field, f.	
E. tasmanicum Hausskn.....	*Cassinia* shrub-land, r.	Probably not cospecific with the Australian species; in fact, the name is applied to a number of distinct high mountain *Epilobia*.
Gaimardia ciliata Hook. f. ..	Bog, la.	
G. setacea Hook. f.	Bog, la.	
Gaultheria antipoda Forst. f..	Herb-field, f.	
G. depressa Hook. f.	Herb-field, f.	Between this and the next species are many hybrids, but none were noted in the new vegetation.
G. rupestris (Forst. f.) R. Br..	Shrubland, o.; herb-field, f.	
Gentiana bellidifolia Hook. f..	Herb-field, r.	

Species etc.	Community.	Remarks.
Geranium microphyllum Hook. f.	Herb-field, o.	
Geum parviflorum Sm.	Herb-field, o.	
Gnaphalium paludosum Petrie.	Bog, o.	
Hebe buxifolia (Benth.) Ckn. & Allan var. *paucibrachiata* Ckn. et Allan.	Herb-field, o.; tussock grass-land f.; bog, o.	
H. subalpina (Ckn.) Ckn. & Allan.	*Dracophyllum* shrubland, f.; herb-field, o.	
H. vernicosa (Hook. f.) Ckn. & Allan var. *Canterburiensis* (J. B. Armstr.) Ckn. & Allan.	Herb-field, f.	
Helichrysum bellidioides (Forst. f.) Willd.	Herb-field, la.	
Hierochloe Fraseri Hook. f. ...	Herb-field, f.	
H. redolens (Forst. f.) R. Br. .	Herb-field, f.	
H. Fraseri × redolens	Herb-field, o.	
Hypolepis millefolium Hook.	Herb-field, o.	
Leucogenes grandiceps (Hook. f.) Beauv.	Herb-field, r.	
Leucopogon Fraseri A. Cunn.	Herb-field, f.	
Luzula campestris DC., un-named var. or vars.	Herb-field, f.	Though various varieties etc. have been described for this great linneon, they are generally incapable of recognition in the field. It seems best to us to treat the easily recognisable jordanons as species, a course adopted to some extent by Hooker.
Lycopodium australianum Herter.	Herb-field, r.	The Australasian representative of *L. Selago* L.
L. fastigiatum R. Br.	Herb-field, la.; *Cassinia* shrub-land, o.	
L. scariosum Forst. f.	Herb-field, la.; *Dracophyllum* shrubland, o.	
Muehlenbeckia axillaris (Hook. f.) Walp.	Herb-field, f.	
Nertera setulosa Hook. f. ...	Herb-field, o.	
Nothofagus cliffortioides (Hook. f.) Oerst.	Herb-field, r.	
Nothopanax Colensoi (Hook. f.) Seem.	Herb-field, o.; shrubland, o.	
N. Colensoi var. *montanum* Kirk.	Herb-field, o.	
Olearia arborescens (Forst. f.) Ckn. et Laing.	Herb-field, o. shrubland, r.	All the species of *Olearia* in this list under favourable conditions assume the tree form.
O. avicenniaefolia (Raoul) Hook. f.	Herb-field, r. shrubland, r.	

Species etc.	Community.	Remarks.
O. cymbifolia (Hook. f.) Cheesem.	Herb-field, r.; shrubland, r.	
O. ilicifolia Hook. f.	Herb-field, r.; shrubland, r.	
O. nummularifolia Hook. f. .	Herb-field, o.; shrubland, r.	
Oreobolus pectinatus Hook. f.	Bog, a.; herb-field, f.	*O. strictus* Berggr. probably also present.
Ourisia lactea Ckn. & Allan, ined.	Herb-field, f.; bog, o.	The *O. Crosbyi* Ckn. of Laing and Oliver's paper (Veget. of Upper Bealey River Basin, Trans. N.Z. Inst. vol. lix, p. 715, 1928).
Ourisia macrocarpa Hook. f. var. *calycina* (Col.) Ckn.	Herb-field, f., shrubland, o.	
Oxalis lactea Hook.	Bog, o.	
Pentachondra pumila (Forst. f.) R. Br.	Bog, la.	
Phormium Colensoi Hook. f. .	Herb-field, a.; shrubland, a.	Leaves much thicker than in the coastal variety and erect.
Phyllocladus alpinus Hook. f.	Herb-field, r.	
Pimelia prostrata (Forst. f.) Willd.	Herb-field, a.; shrubland, o.	
Podocarpus nivalis Hook. . . .	Herb-field, o.	
Polystichum vestitum (Forst. f.) Presl.	Herb-field, f.; shrubland, o.	
Ranunculus Lyallii Hook. f. .	Herb-field, a.	Probably other species of the genus present.
Raoulia grandiflora Hook. f. .	Herb-field, r.	
Schoenus pauciflorus Hook. f.	Herb-field (stream-sides), la.; bog, a.	
Senecio angustatus Ckn. & Sledge, sp. nov.	Herb-field, o.; bog, o.	This species is the var. *angustatus* T. Kirk in Man. N.Z. Flora (ed. 2, p. 1014) It comes true from seed, and is at once distinguished from any form *S. bellidioides* by its much narrower leaves.
S. Bidwillii Hook. f. var. *viridis* T. Kirk.	Herb-field, o.	
S. elaeagnifolius Hook. f. . . .	Herb-field, f.; shrubland, l.	
S. Lyallii Hook. f.	Herb-field (stream-sides), r.; bog, r.	
Wahlenbergia albomarginata Hook.	Herb-field, f. bog, o.	

APPENDIX I

MOSSES AND LICHENS OF NEW VEGETATION AND
ADJACENT NOTHOFAGUS FOREST.

For the following lists of plants the authors are indebted to Dr. H. H. Allan, who was responsible both for the collections and identifications. Whilst the lists are certainly far from complete, they include the most conspicuous and characteristic plants of each area :—

(A) Mosses.

I. FOREST.

Dendroligotrichum dendroides (Hedw.) Broth.	Occasional on forest floor.
Ptychomnion aciculare (Brid.) Mitt.	Abundant on forest floor and on logs.
Acrocladium auriculatum (Mont.) Mitt.	Common on forest floor.
Leptostomon inclinans R. Br.	Forming cushions on tree trunks.
Rhyzogonum mnioides (Hook.) Schimp.	Fairly common on floor, logs, and stumps.
Dicranoloma pungens (Hook. f. & Wils.) Par.	Abundant on floor and logs.

II. THE NEW VEGETATION.

Dicranoloma pungens (Hook. f. & Wils.) Par.	Persisting in depauperate form on ground.
Psilopilum australe (Hook. f. & Wils.) Jacq.	Occasional in damp rock crevices.
Polytrichum juniperinum Willd.	Fairly common on rather dry ground. May be met with on forest margin, but does not enter forest.
Rhacomitrium crispulum Hook. f. & Wils.	Occasional on rocks.
Andraea petrophila Ehrh.	Common on rocks, especially where subject to drip.
Pohlia nutans (Schreb.) Lindb.	Occasional on boggy ground.

(B) Lichens.

I. FOREST.

Usnea longissima Ach.	Abundant on branches of trees and of shrubs fruiting where light is plentiful.
Pseudocyphellaria coronata (Muell.-Arg.) Malme.	Common on tree trunks.
P. dissimulata (Nyl.) Vain.	Occasional on tree trunks.
P. Colensoi (Bab.) Vain.	Occasional on tree trunks.
Sticta filix (Sw.) Nyl.	Fairly common on tree trunks and logs.
Parmelia physodes Ach.	On trunks of trees ; common on trees of outskirts.
Sphaerophorus australis Lam.	Frequent on tree trunks, especially near their bases.

II. THE NEW VEGETATION.

Stereocaulon ramulosum Ach.	Abundant on rocks.
Baeromyces fungoides Sw.	Occasional on bare ground.
Cladonia aggregata (Liv.) Ach.	
C. rangiferina Web.	Among *Dicranoloma* cushions ; occasional also in forest.

APPENDIX II

ALIEN PLANTS OF THE ARTHUR'S PASS DISTRICT.

For the following list the authors are again indebted to Dr. H. H. Allan, who writes, ' . . . . except where noted none of these were seen in indigenous communities. The bulk are road-side plants or occur about the station and village. There are others, especially about the railway station, but I cannot recall them with certainty ' :—

Agrostis tenuis Sibth.	Noted in the grazed parts of tussock grass-land on the Pass as well as elsewhere.
Aira caryophyllea L.	Noted on river-beds, otherwise occupied by indigenous species only, as well as elsewhere.
Alopecurus pratensis L.	
Anagallis arvensis L.	Gardens.
Anthoxanthum odoratum L.	Same remarks as for *Agrostis*.
Barbarea verna Asch.	
Bellis perennis L.	
Bromus hordeaceus L.	
Capsella bursa-pastoris Medic.	
Carex leporina L.	
Centaurium umbellatum Gil.	
Cerastium vulgatum L.	This is interesting as ascending higher up streams than any other alien right into otherwise purely indigenous (open) communities. I have noted the same thing in Westland and elsewhere. In Canterbury, *Stellaria media* also goes well up.
Chrysanthemum Leucanthemum L	
Coronopus procumbens Gilib.	Identification doubtful.
Crepis capillaris Wallr.	
Cynosurus cristatus L.	
Dactylis glomerata L.	
Festuca bromoides L.	
F. rubra L.	
Holcus lanatus L.	
Hypochaeris radicata L.	
Juncus tenuis Willd.	
Lolium perenne L.	
Lotus uliginosus Schkuhr.	
Matricaria suaveolens Buchanan.	
Myosotis strigulosa (Reichb.).	
Nasturtium officinale Br.	Not common.
Plantago lanceolata L.	
P. major L.	
Poa annua L.	
P. pratensis L.	

APPENDIX II (*cont.*).

Poa trivialis L. .... In damp grassy patches, but not at all common.

Prunella vulgaris L.
Ranunculus repens L.
Rubus fruticosus L. (Agg.).
Rumex Acetosella L. .... Gets into open patches of grazed tussock grassland and on loose river-bed.

R. crispus L.
R. obtusifolius L.
Sagina procumbens L.
Sedum acre L.
Senecio vulgaris L.
Trifolium arvense L.
T. dubium Sibth.
T. repens L.
Ulex europaeus L.
Veronica agrestis L.
V. serpyllifolia L.
V. Tournefortii Gmel. ... . Gardens.
Viola arvensis Murr. ... . Noted only near hostel on stream bed.

EXPLANATION OF THE PLATES

PLATE 20.

Fig. 1. Herb-field with *Celmisia Armstrongii* dominant, and bushes of *Dracophyllum longifolium* on right (height 1·2 m.). Other plants present are :—Young *Dracophyllum longifolium, Cyathodes empetrifolia,* and (in right-hand bottom corner) young *Cassinia Vauvilliersii*.

Fig. 2. *Dracophyllum longifolium* succession (average height of bushes 53 cm.) and small piece of *Nothofagus* forest on right, and a dead burnt tree. Spur of Mt. Rolleston in background.

PLATE 21.

Fig. 3. Mass of *Cassinia Vauvilliersii*; in foreground *Danthonia Raoulii* var. *flavescens* or hybrids. Other plants are *Danthonia Raoulii* var. *rubra* and, above *Cassinia* bushes in centre, *Phormium Colensoi*.

Fig. 4. General view of part of area showing bog in foreground, moraine in centre, and upper forest in background. Tussocks of *Danthonia Raoulii* var. *rubra* and var. *flavescens* in foreground.

VEGETATION OF THE ARTHUR'S PASS AREA

VEGETATION OF THE ARTHUR'S PASS AREA

Studies in the Australian Acacias.—I. General Introduction.* By I. V. NEWMAN, M.Sc., Ph.D., F.L.S., F.R.M.S. (late Research Student in Botany, University of Sydney). From the Botanical Laboratories, King's College, London.

[Read 3 March 1932]

INTRODUCTION

At a time when attention was first being focussed on the Leguminosae, de Candolle (1825) declared them to be one of the most remarkable families of plants. Not only have subsequent researches confirmed that statement; but they have shown that the genus *Acacia* is one of the most remarkable genera of the family, due in large measure to the characters of the Australian representatives of the genus. In that country they are most commonly known by the name ' Wattle ' (see Maiden, 1906, for the origin of the name), and by many local names for different species.

The end to which these Studies will be directed is a thorough and complete revision of the genus as it is represented in Australia, for in no other country are the known features of the habit of the genus so fully (almost completely) represented. Apart from the simple interest of recording a co-ordinated description of certain botanical forms, these Studies will be carried out in relation to a number of broad problems centred round the phylogeny of the genus.

Unfortunately, there is still a tendency on the part of some workers to use too static a conception in the practice of taxonomy. So long ago as 1875, Bentham pointed out that there had been a greater division into species of the Compositae than of the Cassieae or Mimoseae, simply because material of the Compositae was more available, so that workers had the opportunity to diagnose new species upon minute differences. This condition of things is only possible when the conception of taxonomy is too static. At the present time, the genus *Acacia* is in danger of the same fate. In the present study, a scheme of classification will be suggested embodying a kinetic conception of the subject; and it is hoped that ultimately the Australian Acacias will be fitted into that scheme or a modification of it. Bentham further suggested that the Mimoseae are descended from a common stock which was broken up by geographical changes. Finding the origin of the Australian Acacias should lead in the direction of that common stock.

Beyond the discovery of morphological novelties in it (always possible in a large field of research), the genus has an interest because it falls within the

* Thesis (in part) approved for the degree of Doctor of Philosophy in the University of London.

province of several recent morphological theories, e.g. the theory of carpel polymorphism, enunciated by Miss E. R. Saunders (1929) ; the phylloclade theory of the legume, by Prof. J. McLean Thompson (1929) ; a theory of derivation of various forms of branching, by Prof. W. Zimmermann (1930), etc. There is also the relatively untouched palaeontology of the genus.

This introductory Study will serve as a guide to the starting-points from which various branches of the literature on *Acacia* can be followed. In connection with macroscopic observations, two series of papers should be particularly mentioned—J. H. Maiden's ' Notes on *Acacia* (with description of new species) ', 1915, and R. H. Cambage's ' *Acacia* Seedlings ', 1915. Microscopical observations on the morphology of reproduction in *Acacia* appear to be entirely lacking since 1880, before and about which time there were three chief papers—by Rosanoff (1865), Engler (1876), and Guignard (1881). An entry to the literature of fossil Acacias will be found in a work by E. W. Berry (1916).

Because this Study is only introductory to a revision, the discussions are not always carried through to a conclusion, being frequently concerned only with pointing out the significance of certain phenomena or certain lines of inquiry to be studied at a later date.

DIVISION OF THE LEGUMINOSAE

United to the other Leguminosae by the common possession of the legume, the Mimoseae can be separated from them along more than one line. De Candolle (1825) made the following division :—

```
                          LEGUMINOSAE
        ┌──────────────────────┴──────────────────────┐
  Curvembriées.                              Rectembriées.
  (Radicle bent back on the                  (Radicle straight.)
  commissure between the
  cotyledons.)
  ┌──────────┴──────────┐              ┌──────────┴──────────┐
Papilionacés.        Swartziées.     MIMOSÉES.          Césalpinées.
(K. separate, A. perig.,  (K. united, A. hypog.,  (K. and C. valvate,  (K. imbricate,
  C. papilionate.)         C. 0.)                   A. hypog.)           A. perig.)
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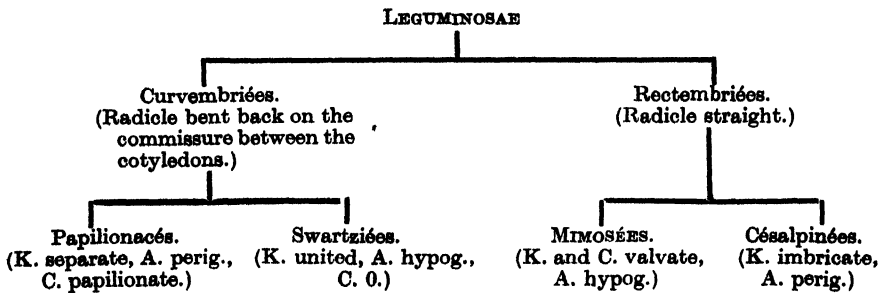
Taubert (in Engler and Prantl, 1894) separates the Mimosoideae (Mimoseae) in one double step :—

```
                    LEGUMINOSAE
        ┌───────────────┴───────────────┐
  MIMOSOIDEAE.                  Caesalpinioideae and Papilionatae.
  (Actinomorphic, C. valvate.)  (Zygomorphic, C. imbricate.)
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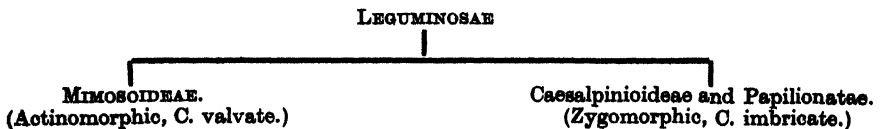
The genus *Acacia*, in the Mimosoideae, is therefore to be found among the Leguminosae having the following characters : actinomorphy, valvate corolla, hypogynous androecium, straight embryo.

DIVISION OF THE MIMOSOIDEAE

De Candolle included the following genera :—(After Willdenow) *Mimosa*, *Schranckia*, *Inga*, *Acacia*, *Desmanthus* ; (after Richard) *Entada* ; (after Kunth) *Prosopis*, *Adenanthera* ; and himself added *Gagnebina* (Necker) and *Darlingtonia*.

Bentham (1875), in his revision of the Natural Order, divides it into three great tribes and four small ones. Taubert (1875) follows Bentham, except that he places *Pentaclethra* and *Parkia* in the one tribe (Parkieae) separated from the other tribes by having an imbricate, instead of a valvate, calyx :—

MIMOSOIDEAE

| Parkieae. Piptadenieae. Adenanthereae. | Eumimoseae. (Definite stamens.) | Acacieae. (Indef. st., free.) | Ingeae. (Indef. st., united.) |
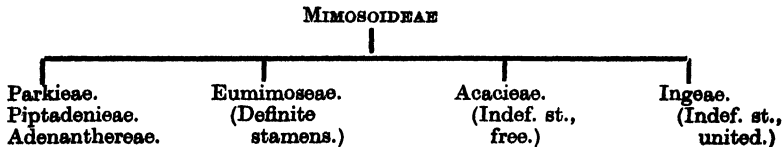
DIVISION OF THE ACACIEAE (ACACIA)

Previous workers seem to have made the first one or two steps of their division of the genus on the vegetative characters, leaving the reproductive features as apparently minor factors in the development of the various lines of descent. Bentham bases his sections on the vegetative habit (for several steps of division, in some sections). He makes six sections :—

ACACIA

| Phyllodineae. | | Pulchellae. | | Vulgares. |
| | Botryocephalae. | | Gummiferae. | | Filicinae. |
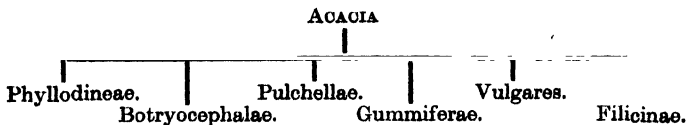
The first has its leaves reduced to phyllodes (in some cases now recognised as phylloclades) and includes more than half of the Australian species. The other five are bi-pinnate, and are separated from one another chiefly on vegetative features with occasional use of inflorescence characters. The sub-sections of the Phyllodineae are made on foliar features. In the division of *Acacia* Taubert follows Bentham. Moore and Betche (1893), Maiden and Betche (1916), and Black (1929) also follow, in general, Bentham's classification, with slight changes due to the greater number of species known and to the different and incompletely known composition of the genus in the several areas they survey. In all these classifications the inflorescence takes a secondary place. In South Africa, Glover (1915) uses the stipules as the first principle of division. The classifications referred to give the impression of being concerned with the terminal representatives of an extinct group, rather than with a living and developing phylum.

In making these criticisms, the writer recognises the complexity of taxonomic work, and that the apparently static conception referred to has been due to the incompleteness of our knowledge and to the restrictions enforced by the requirements of local floras. This matter will be returned to in the discussion of the classification suggested in a later part of this Study.

DISTRIBUTION OF ACACIAS

Of the Mimoseae, Bentham recorded only four that were indigenous, without doubt, to both the old and the new World : *Entada scandens, Nepuntia oleracea, Mimosa asperata,* and *Acacia farnesiana. A. farnesiana* was the only one that also occurred in Australia. He regarded aquatic means of migration as being possible for the other three, but could find no explanation of the distribution of *A. farnesiana.* No other *Acacia* species are found in every continent that is occupied by the genus. Europe is the only large geographical area devoid of the genus ; and there are no species in New Zealand, despite its relative proximity to Australia. There are some seven hundred species known, of which some five hundred are endemic to Australia, and even four hundred of these belong to the section Phyllodineae (Andrews, 1914). The Acacias manifest a high degree of endemism, both of sections and of species—and that endemism is particularly frequent in Australia.

The distribution of the genus is as follows, the statements of locality being taken from Andrews, combined with the numbers of species (after the locality) from Bentham :—

Gummiferae.—America (17), Africa (35), Asia (9), Tropical Australia (4).

Vulgares.—America (42), Africa (23), Asia (9).

Filicinae.—Central America (2).

Botryocephalae.—Endemic in Eastern Australia (10, but many more since described).

Pulchellae.—Endemic in Western Australia (8).

Phyllodineae.—Endemic in Australasia (275). (Andrews gives 400, and a few ' waifs ' in neighbouring islands.)

Bentham's totals are :—America, 61 ; Africa, 58 ; Asia, 18 ; Australasia, 297 ; Grand total, 434. Andrews says there are about 700 species.

Acacia species are recorded from the Tertiary floras of North America and Europe. But the strangest thing is that phyllodineous Acacias are reported. Unger (1865) refers to phyllodineous Acacias in Europe, during the Eocene. Berry (1916) establishes a species, *A. Wilcoxensis,* on the evidence of one leaf impression, refers to it as between the leaves of the living species *A. oblunata* and *A. pycnantha,* and compares it with four other phyllodineous species described by Ettingshausen (1853) from the Tertiary of the Tyrol in Europe ! Berry also refers to species of *Acacia* in the grés de Belleu of the Paris basin (France), and from the Isle of Wight.

The conclusion that the phyllodineous Acacias were present in the Eocene of North America and Europe is very doubtful, in view of the scanty evidence (sometimes only a single leaf-impression), and of the unlikelihood that such a vigorous group of plants, as the phyllodineous Acacias show themselves to have been, should be completely extinguished in the northern hemisphere.

HABIT AND INTERNAL CONSTRUCTION

The habit of the genus shows an extraordinary variety. Some species are barely more than 15 cm. high, while others are forest-trees of some hundred feet. Some have a soft and feathery foliage, while others have the phyllodes developed as sharp thorns, and still others are lacking in foliar structures at all. Some grow in cool glades by water-courses, and some in arid deserts. The inflorescence may be composed of globular heads or cylindrical spikes; the heads may be paniculate, racemose, or solitary. Many of the theoretically possible associations of inflorescence and foliage forms can be found in the field.

Cambage (1915) found in sixty species (with four exceptions) that, whatever be the adult foliage, the first leaf after the cotyledons was simply pinnate and was followed by abruptly bipinnate leaves. In the Phyllodineae, these gradually progress into true phyllodes. The transition to phyllodes may be considerably delayed in some species.

The internal construction of the plants is so little known that it is impossible at present to associate it with any divisions of the genus. It would be instructive to compare Cambage's papers on the seedlings with Peters's paper (1926) on the anatomy of the *Acacia* phyllodes.

The common features of habit are referred to later. With regard to the internal morphology of reproduction, apart from normal features, the phenomena common to the Acacias seem to be the indefiniteness of the number of megaspores (Guignard, 1881) and the association of the pollen-grains in pollinia.

A PHYLOGENETIC CLASSIFICATION

Earlier in this Study, objection was taken to existing classifications of the genus *Acacia* as being too static in conception and too much like analyses of a collection of objects. These systems have been based on the foliage or other vegetative features for the principal divisions. Since the reduction to phylloclades is the extreme limit in the line of foliar modification, a classification based on the foliage could not show evolutionary change after the phyllocladineous condition had been attained so clearly as one based on features susceptible of more prolonged or of repeating changes. Relationships rather than forms of organs would provide this susceptibility. Such relationships are well founded in the reproductive structures, which also have the advantage of conserving more frequently the vestiges of past history. The changes in the relationships between the flowers in the flower-groups, between the flower-groups in the inflorescence, and between the inflorescence and the vegetative axis can be repeated (theoretically) again and again. Principal divisions along these lines will therefore be more likely to provide a truly phylogenetic scheme of classification. These Studies will attempt to classify the Acacias (particularly as they are found in Australia), firstly, on the inflorescence and, secondly, on the flower-groups, the foliar characters being introduced not earlier than the third principle of division. Such a scheme of classification

is shown below. Alternative names for the Phyllae, Phyllodineae, and Phyllocladineae are Bipinnatae (in recent flora only), Petioles, and Caules.

The following morphological classification of the genus *Acacia* is based on Inflorescence, Flower-groups, and Foliar types :—

I. Racemoseae. (Inflorescence in racemes.)
II. Constateae. (,,   clustered.)
III. Singulares. (,,   single.)

Each of these is divided according to the flower-shape :—
i. Spicateae. (Flowers in cylindrical spikes.)
ii. Oblongae. (,,   in oblong spikes.)
iii. Globulae. (,,   in globular heads.)

A further sub-division of each of these depends on the foliar type :—
1. Phyllae. (True leaves. Bipinnate in adult of present day.)
2. Phyllodineae. (Petioles without laminae in adult.)
3. Phyllocladineae. (Entire absence of leaves.)

Such an arrangement shows that the forms which are usually grouped as Phyllodineae are not monophyletic except far back in the course of descent, and possibly never were so, as ' Phyllodineae '. The polyphyletic condition of the ' Phyllodineae ' is supported by their great numbers and the really diverse forms of phyllodes among them. In comparison, it is to be noted that among the ' Phyllae ' (Bipinnatae) there are recognised three distinct sections : the Gummiferae in the tropics, the Botryocephalae endemic in East Australia, and the Pulchellae endemic in West Australia.

But even yet, the above scheme does not adequately represent the possibility of evolutionary progression, suggesting an analysis of a collection of forms, rather than the presentation of a series of lines of descent, of which a present-day classification would be a cross-section. For the impression given is that the several Phyllae, Phyllodineae, and Phyllocladineae sections are the end-products of the lines, and that they (the Spicateae, Oblongae, Globulae, and the Racemoseae, Constateae, Singulares) form three equally tripartite groups. It seems more probable that the relation in each group is not one of equality but of transition : from racemes through clusters to solitary heads, from cylindrical spikes through oblong ' spikes ' to globular heads, and from true leaves through loss of lamina with functioning of petioles to loss even of petioles. Whereas the foliar transition comes to a stop with the phyllocladineous condition, the inflorescence and flower-group transitions can be repeated. Though it seems possible for both latter lines of transition to proceed independently, the inflorescence, at any point in its transition, is a whole of which the flower-groups (whatever be their point of transition) are parts. Consequently, in postulating a phylogenetic classification, the first line of transition will be taken to be in the inflorescence. At any point in that

line, secondary lines of transition, in the flower-groups, could begin. And at any point in these secondary lines, tertiary lines of transition, in the foliage, could begin. In such a Phylogenetic Classification the genus is represented as derived from an ancestral type having a racemose inflorescence of cylindrical spikes and with true leaves.

From the ancestral type, one line of transition proceeds by means of the reduction in growth of the inflorescence axis through the Constateae to the Singulares, and beyond that, by the diminution of the vegetative axis and the subtending foliar organs, to the racemose condition again.

From any point in this line, a secondary line of transition could proceed, by condensation of the flower-group, through the Oblongae to the Globulae. Beyond that, by reduction in growth of the axis of the flower-group with modifications in the inflorescence or vegetative axes and subtending organs, further transitions can take place.

The tertiary line of transition, which can take place from any point in the secondary lines, is by way of elimination of the lamina of the leaf through the Phyllodineae to the total suppression of the leaf in the Phyllocladineae.

Considered theoretically, there are many cross-transitions possible between the tertiary lines. For instance, the Racemoseae–Spicateae–Phyllodineae could change to the Racemoseae–Oblongae–Phyllodineae. A little thought would soon make the scheme bristle with cross-lines of transition in extraordinary complexity. That very complexity conforms with the great variety in the habit and distribution of the genus, and offers a reason for the difficulty often experienced in placing species of *Acacia*. But, though potentially so complex, this scheme, in my opinion, opens a road to the clear understanding of the genus. In this classification place is not found for the differences in similar leaf-types, e.g. micro- and macro-pinnulate bipinnate leaves, broad and narrow uni- and pluri-nerved phyllodia, and between pentamerous and tetramerous flowers, &c. A reason would be provided for a phenomenon such as recorded by Babcock (1924) in the genus *Crepis* : two species (*C. capillaris* and *C. tectorum*), regarded as being ' very closely related ' by taxonomists, were found to be inter-sterile, but were each inter-fertile with *C. setosa*. Such a phenomenon might be expected to occur between two species taxonomically similar, but on different tertiary lines of transition, and a third species situated on either line nearer to the point of divergence.

The classification presented covers for the three features the whole theoretical ground of the genus *Acacia*. But it is not intended to suggest that all the lines of descent have been followed in the course of Nature, or that all those which have been followed have been brought to the stages shown in the scheme, or that none have gone beyond. The phylogeny proposed would be an outstanding example of parallel evolution. The scheme is offered as a first approximation which will undoubtedly be changed by future investigations.

Although the amount of literature consulted has been relatively very small, yet several matters have come to attention in support of the scheme. The

climate of the whole earth in the Tertiary period was more uniform and tropical than it is to-day. Andrews (1914) points out that the uniform and less specialized species of *Acacia* are diffused throughout the tropics, while the specialized forms have developed locally outside the tropics on various lines (largely foliar reduction in Australia). Certainly, some tropical species show a condition describable as specialization, such as the large, spinescent, ant-inhabited stipules of the bipinnate 'bullhorn' Acacias, e.g. *A. melanoceras*, &c., of the Panama Canal Zone (Standley, 1928). But such a specialisation is incidental and relatively unimportant, compared with a line of specialization which culminates in the entire loss of leaves for the adult condition. Bentham suggests the south migration of the genus. With this was a frequent change from true leaves to phyllodes, a change confined to Australia. The only phyllodineous Mimoseae outside Australasia, recorded by Bentham, are four species, not *Acacia*, in tropical America ; so that scarcely any deviation from the ancestral condition has occurred in the relatively unchanged tropical environment.

Beyond these facts, there is the evidence of *Acacia* seedlings with their juvenile bipinnate leaves, preceded usually by one pinnate leaf, whether the adult foliage be bipinnate, phyllodineous, or phyllocladineous (Cambage, 1914, 1915). Peters (1926) has described anatomically, step by step, the metamorphosis of leaf-stalks into leaves (Blattstiel–Blatt–Metamorphose), in the ontogeny of living individuals. All this supports the Phyllae–Phyllodineae–Phyllocladineae lines of transition.

It may be that even in the Phyllae three steps will have to be made. Zimmermann (1930) instances *Acacia* leaves as belonging to the feathery (' fiedrige ') type of branching with opposite lateral organs (' mit geganständigen Seitenorganen ') ; and derives them from the feathery type with alternate lateral organs by these moving together in pairs (' durch paarweises Zusammenrücken '). This process corresponds to what I have called ' condensation ' in the inflorescence. If, in the distal region of an alternate system of simply pinnate leaves, this condensation took place, opposite, simply pinnate leaves would be found on an alternate branch system. Further condensation in the distal region of this system could form alternate bipinnate ' leaves ' which really had the nature of branch systems, and had changed outwardly from radial branching to branching in one plane (apparently dorsiventral). Zimmermann refers to Peters's (1927) description of *radial* steles in the rachis (' Spindel ') of the feathery leaves of many *Acacia* species.

Cambage (1915) records the occurrence of a pair of opposite pinnate leaves between the cotyledons and the bipinnate leaves in four species, and, from this and the normal recapitulatory evidence, considers the ancestral sequence to have been : opposite-pinnate→alternate-pinnate→alternate-bipinnate. But, in my opinion, it seems quite possible that, in a phylogenetic process of condensation, as suggested above, recapitulation might show either only one pinnate leaf or only a pair of opposite pinnate leaves. The test would be the sequence, if a species could be found with both alternate and opposite-pinnate leaves in the seedlings.

The forms of the inflorescence have not been so fully studied as those of the foliage ; but, from them also, there is some support for the suggested classification. The most modified foliage (Phyllocladineae) is associated with the absence of the most primitive inflorescence (Racemoseae) (viz. *A. continua*). Sometimes, terminal recemes appear by the abortion of the leaves subtending solitary flower-heads near the end of a branchlet (e.g. *A. complanata*). Evidence shows that the globular head is a condensed spike.

MATERIAL

Having in view the classification proposed in this Study, a selection of what were considered to be significant species was made for examination. Because certain of the first group of the Botryocephalae not only are of economic value, but also are variable and are suspected of natural hybridization, they were selected in greater proportion, and taken as the starting-point for the morphological and cytological investigations. In making the selection, attention was given to species having varieties, to those showing contrasts in habit, and to some obviously transitional forms. In the following list, the flowers are pentamerous, except where stated :—

LIST OF SPECIES FOR EXAMINATION

Racemoseae	Capitateae	Phyllae	*Baileyana.*
			discolor (+vars).
			decurrens (6 vars.).
			adenophora (various forms).
			elata.
		Phyllodineae	*buxifolia* (+vars.).
			linifolia (+vars.).
			pinninervis (+vars.).
			myrtifolia (4 calyx).
		Phyllocladineae (?)	*restiacea.*
Constateae	Spicateae	Phyllae	*Drummondii.*
and Singulares ..	and Oblongae.		
		Phyllodineae	*longifolia* (tetramerous).
			florabunda (tetramerous).
			(2 vars.).
			oxycedrus (tetramerous).
			linearis (tetramerous).
			glaucescens.
			dorothea.
	Capitateae	Phyllae	*Farnesiana.*
			Bidwillii (tetramerous).
			pallida.
		Phyllodineae	*juniperina* (+vars.).
			lanigera (+vars.).
			trinervata (+vars.).
			undulifolia (+vars.).
			diffusa (tetramerous).
			stricta.
		Phyllocladineae (?).	*continua.*
			spinescens.
			tetragonocarpa (tetramerous).

Transitions :—Complex; simple racemes .... *ixiophylla.*
              Singul. capit.; racem. capit. .... *complanata.*
              Racem. capit.; singul. capit. .... *venulosa.*
                                             elongata.
                                             farinosa.
                                             melanoxylon.
                                             calamifolia.
              Spicateae : Capitateae.................. *Burkittii* (tetramerous).
              Phyllae : Phyllodineae .... *rubida.*
                                             melanoxylon.

SUMMARY

In the studies to which this paper is an introduction, the genus *Acacia* ('Wattles', in Australia) will be carefully revised, the aim being to establish a phylogenetic classification of the genus as it occurs in Australia.

Previous classifications are regarded as too static in conception. These Studies will seek to develop a kinetic conception.

Features of the genus have a bearing on the theories of carpel polymorphism (Saunders), phylloclade legume (Thompson), leaf forms (Zimmermann).

The position of the genus *Acacia* in the Leguminosae is briefly reviewed.

The existing classification of the genus is found to be usually made with foliar or other vegetative features as the first principle of division. This is regarded as unsatisfactory.

The contemporary and geological distribution of the genus is briefly reviewed.

The variety of the habit of the genus, the recapitulatory features of the seedlings, and the common morphological features are referred to.

An attempt is made to formulate a phylogenetic classification, based on the relationships of the flower-groups in the inflorescence as the first principle of division, on the relationships of the flowers in the flower-groups as the second principle of division, and on the foliar character as the third principle of division. The theoretical considerations underlying this scheme are presented, together with some already-known phenomena of the genus which support it. The scheme explains the occurrence of difficulties experienced in placing species in existing classifications.

There is given a list of species selected for examination.

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Studies in the Australian Acacias.—II. The life-history of *Acacia Baileyana* (F. v. M.). Part I. Some ecological and vegetative features, spore production, and chromosome number.* By I. V. NEWMAN, M.Sc., Ph.D., F.L.S., F.R.M.S. (late Research Student in Botany, University of Sydney). From the Botanical Laboratories, King's College, London.

(PLATES 22-25, and 16 Text-figures)

[Read 3 March 1932]

INTRODUCTION

Acacia Baileyana (' Cootamundra Wattle ') was first described by Baron Ferdinand von Mueller (1888 a). He separated it from *A. polybotrya* on material supplied from a tree in cultivation at Bowen's Park, Brisbane.

In beginning an inquiry into a genus so little known in its morphology, anatomy, and ecology, it seemed desirable to study one species in detail. *Acacia Baileyana* was chosen because it seemed to be a really distinct species, despite a little variation within itself ; it stands at one end of a series of species which includes the economically important *decurrens* group (or varieties, as some taxonomists think) ; and, since having been cultivated, it has been thought to have given rise to hybrids with that group.

The present paper deals with ecology, habit, floral structure, and the reproductive processes up to the formation of the spores. Cytology is included only where necessary for establishing the course of morphology, and the chromosome number. Methods of study have distinctive features for any one genus. As this enquiry is evolving such methods for the genus *Acacia*, much of it will be suggestive rather than conclusive.

Moore (1893) places *A. Baileyana*, together with *A. elata*, *A. pruinosa*, *A. discolor*, *A. spectabilis*, and *A. polybotrya*, in Undersection 1 of the Section Bipinnatae, which, with Undersection 2, is included in Bentham's Series Botryocephalae. *Baileyana* was not separated from the widely distributed *polybotrya* till Mueller (1888 a) did so, chiefly on account of its restricted distribution, glabrous leaves which are more compact, glands on the rachis, broader fruit not constricted, and other characters. Moore (1893) separates it from *pruinosa* also by the glands on the rachis. In the tentative classification, suggested in No. I of these Studies, *A. Baileyana* and its associated species would fall in the Racemoseae–Globulae–Phyllae Section (Newman, 1931).

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* Thesis (in part) approved for the degree of Doctor of Philosophy in the University of London.

MATERIAL AND METHODS

The material for the present enquiry was taken, between 22 and 24 July 1929, from two trees in cultivation at Strathfield, Sydney, N.S.W. : three lots between 9.30 a.m. and 12.30 p.m. and one lot between 4.30 and 5.30 p.m.—there was warm sunshine on all occasions. Tree No. 1 is glabrous, No. 2 is pubescent. The material upon which this paper is mainly based consists of buds up to half size, taken from Tree No. 2, except that any stages later than about division of the microspore or the formation of the megaspores are in material from Tree No. 1. At the time of collection, Tree No. 1 was approaching full bloom and Tree No. 2 had scarcely begun. Those youngest stages still showing seemed to have been in a state of arrested development, so that it was impossible to find good examples of the archesporia in the anther and of the beginning of the ovule. Confirmatory material was taken at Kew Gardens * ; and, though appearing to have suffered badly from the climate, it did not suggest anything contrary to what was found in the Australian material. The Kew material was collected in early January 1930.

The late Professor A. A. Lawson of Sydney used to crush the young flower-heads in the killing and fixing fluid, to obtain immediate penetration. This has not been done for the present investigation, but it is recommended that for purely cytological study material be slightly crushed in the fluid. The stains used were Heidenhain's iron alum haematoxylin and its modification by differentiating with acid 70 per cent. alcohol, also various combinations of safranin, gentian violet, light green and orange G. Several special methods of examination will be described in connection with the presentation of their results. The constituents of the fixatives used are given, together with the numbers of certain figures from material variously fixed :—

Fluid A. Chromic Acid, Acetic Ácid, Osmic Acid, Water.

„ B. Mercuric Chloride, Acetic Acid, Formalin, Alcohol, Water.

„ C. Picric Acid, Formalin, Acetic Acid, Urea, Chromic Acid, Water.
(Allen's modification of Bouin's fixative.)

„ D. Alcohol, Formalin, Water.

Material for A and C was plunged into 90 per cent. alcohol and then in water before fixing.

With regard to perianth and carpels :
D was used for figs. 27, 37–9.
B was used for figs. 26, 28, 33, 36, 40.

With regard to the nucleolus in mother-cells :
A was used for fig. 51. C for figs. 50, 59.
D was used for figs. 46, 57.

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* The writer expresses his thanks to the Director for permission to collect this material.

OCCURRENCE

The species is found wild only in a comparatively small district, about
75 miles long by 60 miles broad, towards the south-east of New South Wales,
Australia (text-fig. 1).   Mueller, in the first description, reported it from
near Cootamundra, ' on one source of the Murrumbidgee ' River ; from To-
morrow, on a tributary of the Lachlan River ; from Wagga Wagga ; and
stated that it occurred on ' stony ridges '.   Maiden (1906) records it from

TEXT-FIG. 1.
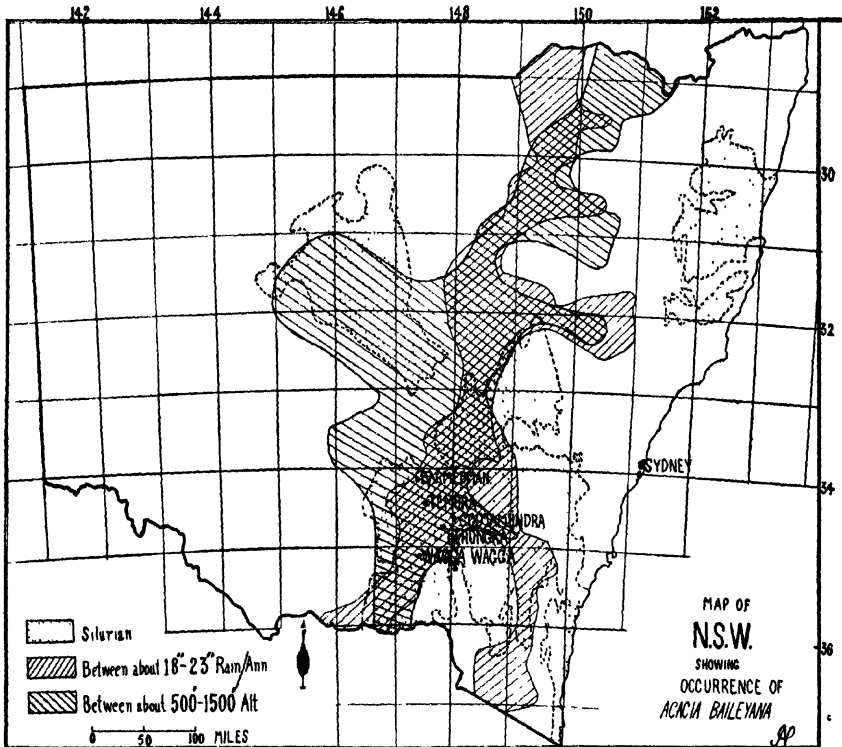
Map of New South Wales, showing distribution of *A. Baileyana* in association with three
features of habitat—geological, rainfall, altitude. The names of the towns (except
Sydney) are the localities where the species is reported to occur naturally. For
explanation, see text. Compiled from maps and literature.

Bethungra, Temora, and Barmedman.   Cambage (1902) concluded its distribu-
tion, before cultivation, to have been within a circle of radius about thirty
miles, between Cootamundra and Temora.
The locality where *A. Baileyana* is found is characterised by the conjunction
of the following (text-fig. 1) :—An area of Silurian rocks (associated with

some patches of Igneous rock—granites and porphyries), an altitude of from 500 ft. to 1,500 ft., and an average annual rainfall of between about 18 and 23 inches. The area of this conjunction is a little larger than the dimensions given below. The only other area in New South Wales of similar conjunction is a smaller one, immediately to the north, separated from the first by an eastward recession in the boundary of the Silurian rocks and a westward advance of higher land. Before any definite conclusions could be drawn, it would be necessary to make a detailed geological examination of the area concerned, and to survey the local distribution of the species.

The present reference is made as being indicative of one of the avenues of inquiry from which indications of the relationships of species might be sought.

Though of no economic importance, the tree is much cultivated in Australia for its beauty, and has been introduced into England, the Americas, and the south of Europe.

HABIT AND INFLORESCENCE

The general appearance of the tree in early autumn—April (in Sydney)—in shown in Pl. 22. fig. 17. The young racemes of flower-heads hang like a beard from the ultimate branches. The flowers will not open till late July. The extremely glaucous foliage (Pl. 22. figs. 17, 18, 19, & 22) gives the tree a blue-grey colour. The height is usually between 5 and 8 metres. There seem to be two types—glabrous and pubescent, though the floral bracts in both have hairs.

The details of the habit are mostly described by Mueller and Moore, and are beautifully figured by Mueller (1888 b).

At present, the species has a slight variability, which may be due to hybridization in areas where it is cultivated. For instance, the eight leaves in fig. 22, typical specimens from eight trees at Kew Gardens, might quite well come from seed of one tree in cultivation. Leaves a and b are the most typical Baileyana leaves, while h is certainly not a Baileyana leaf. The direction of rotation of the phyllotaxy is sometimes clockwise and sometimes anti-clockwise (Pl. 22. figs. 18, 19). The anti-clockwise rotation is the more common ; and both may be found on the same tree. On some branches, the upper leaves have one pair of pinnæ the less, while it is the lower leaves on other branches.

The phyllotaxy of the raceme is 2/5, and may be both anti-clockwise and clockwise on the same branch (Pl. 22. figs. 18 & 19). In the later-formed racemes there is a tendency to increase the frequency of the aberration of the number of members in the perianth-whorls of the upper flower-heads.

The unopened flower-heads, containing from twelve to twenty flowers, are globular and about 2–3 mm. in diameter. At anthesis, the coiled filaments straighten, so that the anthers are much exserted, the diameter of the head appearing to be about 5–7 mm. Each young flower is enclosed by its subtending bract (Pl. 22. fig. 20 ; Pl. 23. fig. 25) till the head is about half-size (cf. lengths in Pl. 23. figs. 26 & 27). A curious feature is the ' pith ' of large cells which

appear tabular in longitudinal sections of adult heads. This tissue, very strongly developed before the vascular bundles of the head and flowers are organized, probably serves a conducting function in the early stages (Pl. 22. fig. 20 ; Pl. 23. figs. 25–27). It differs from ordinary parenchymatous tissue in the shape of the cells and in the thick walls, which stain heavily.

There does not seem to be any definite distribution of sterility among or within the flower-heads. Complete gynoecial sterility of the whole head is not unusual ; while complete fertility is not frequent. The styles of only fertile carpels being exserted, the appearance of the opened head varies with the degree of gynoecial sterility.

The flowers are in slightly spaced groups of five. Each group is regarded as being disposed in a low spiral with a divergence of 2/5. The members of each group alternate with those of the adjacent groups, giving the appearance of ten vertical rows. The heads were analysed by means of serial longitudinal and transverse sections, and by the construction of a model in modelling material and drawing-pins. The transverse section showed the groups of five, the members of successive groups alternating (Pl. 24. fig. 24). From the serial longitudinal sections the position of the flowers was plotted on a circle representing the vertical projection of the axis, the result suggesting the arrangement of the flowers in ten vertical rows. The model was made as follows :— A flower-head (unopened) and a cylinder of modelling material, of calculated diameter, were placed on vertical axes. The flower-head being placed with the lowest flower straight to the front, a drawing-pin was put straight in the front of the cylinder of modelling material. By equal rotations of the two axes, and the placing of pins to correspond with flowers, the rough model shown in fig. 23 was made. It confirmed the interpretation of groups of five with the alternation of members of successive groups. When there are under twenty flowers on the head, there will be one or more vertical rows with only one flower. The spiral arrangement of the flowers in the groups was strongly suggested during the analysis, and is inferred from theoretical considerations (see later). To show this point with precision, serial sections at not more than 4μ thickness would be required of very young flower-heads (for demonstration of uncompleted spirals). The medulla of the pedicle is five-rayed, in transverse section (Pl. 22. fig. 21), a condition that can be seen also in the axis of the flower-head—making allowance for the overlapping of the stelar flower-gaps.

There is evidence that occasionally the head may be built on a divergence plan of four, instead of five.

The method of terminating the flower-head appears to have been by a cessation of apical growth soon after some organ had been initiated—flower or bract (Pl. 23. figs. 25–27). An example was observed where four of the flowers in the final whorl had failed to develop in the axils of their bracts. Other variants have been seen.

The general impression given by the variability of the habit is of a species in a labile condition. Not only are there glabrous and pubescent sections

TEXT-FIG. 2.
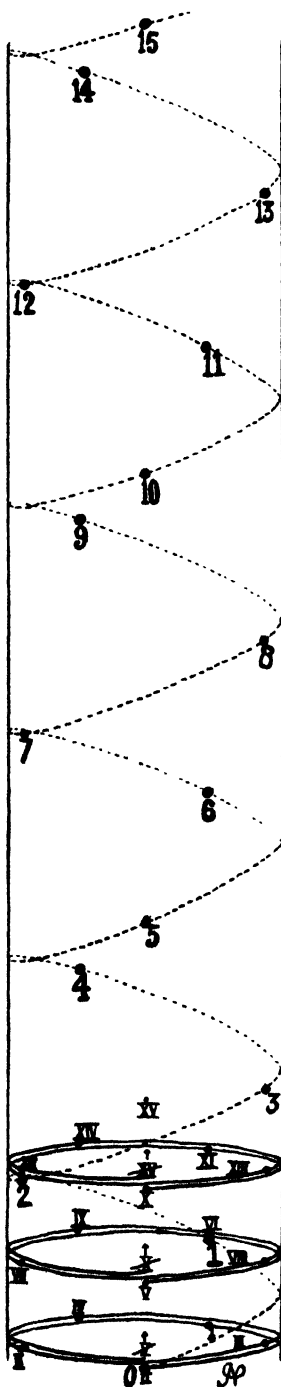
EXPLANATION OF TEXT-FIG. 2.

Diagram illustrating the condensation of a spike into a head. Dotted line and arabic numerals represent the flower and spiral on a spike (2, 5 divergence); the continuous line and roman numerals represent the corresponding spiral broken in condensation. For explanation, see text.

of the species, but there seem to be two sections with mostly three and mostly four pairs of pinnæ on the leaf. (See also the description of two or three pairs of pinnae, given by Clos (1929) for the species as cultivated in Argentina.) The indefinite number of flowers in the heads, the failure of some of the flowers in the terminal whorl to develop, and the termination of the head, not by any definite organ, but just by cessation of its axial growth, suggest a diminution of growth, which, with shortening of the raceme axis, could produce a spike—as suggested in Study I. The different directions of rotation in the phyllotaxy may be due to conditions of crowding &c. that are purely local on the plant.

From the evidence given above, and the following theoretical considerations, the flower-head of *A. Baileyana* is regarded as having evolved from a spike with a phyllotaxy of 2/5. In text-fig. 2, the broken line represents the imaginary spiral through 16 flowers (0–15) arranged, with a 2/5 divergence, along an axis. The ' condensation ' of a spike can be regarded as a shortening of the interval of time or of linear growth between the laying down of successive primordia, when the principle of correlation has been changed. The limit to this shortening of the interval, if not determined by a maximum possible variation in the correlation, will be determined by mechanical needs of space. In this theoretically condensed spike, the first flower (0) having been laid down, there seems to be no reason why flowers I, II, III, IV should not arise on the low spiral represented by the continuous line. But, when flower V comes to be laid down, the needs of space will require a larger interval of growth to take place. Therefore a second and similar low spiral with flowers V–IX will be formed at a little distance from the first one ; and subsequently a third, comprising

flowers X–XIV. If the limiting factor in condensation is only spatial, a little more shortening could be had if flower V was laid down, not vertically above flower 0, but above the gap between flowers 1 and III and the remainder of the group similarly displaced ; the third group could remain on the original vertical lines, or follow the small rotation started by the second group (so that X would be vertically above III). The result would be a series of slightly separated low spirals, each containing five flowers at a 2/5 divergence, and with the flowers of successive spirals alternating, to give the appearance of ten vertical rows. Such a condition was recorded in the foregoing description.

THE FLOWER

The young thalamus grows so rapidly that, by the time the stamens are due, it is in the form of a solid cylinder with the sepals attached to its base and the petals half way up its side (text-figs. 3 D, E ; Pl. 22. fig. 20 ; Pl. 23. fig. 25). The slight depression in the apex may be due to the rapid growth of primordia, rather than to any special form of the thalamus. The normal sequence is observed, the numbers of parts being usually K 5, C 5, A 40–50, G 1. Occasional variations of the number of sepals and petals are found (4 and 6), particularly in the inflorescences last developed. Text-figs. 3 C & 3 D were selected as they showed this feature.

The members of the sepal and petal whorls do not arise simultaneously, and the impression is given of spiral sequences. Text-figs. 3 A, B, & C show uncompleted whorls with differences in size of the parts already being formed. The first formed (outer) stamens arise opposite the sepals (text-figs. 3 D & 3 E). The carpel arises approximately above the large-celled pith, grooved towards the axis (text-fig. 2 F ; Pl. 24. fig. 33).

The apparent spiral origin of the parts of the flower, the slight variation in the numbers of the petal and sepal members, and the foliar nature of the carpel, support the theory that the flower is essentially of the same nature as the vegetative shoot—a metamorphosed shoot, as formerly described. Zimmermann (1930) supports this similarity, describing it as parallel formation (' Die Gesamtsporangienstände, die Blüten, sind Parallelbildungen zu den vegetativen Sprossen . . . '). In a system which is fundamentally a modified spiral structure with periodic changes of form in its ontogeny, the formation of one member the more or less before a point of change would be more likely than in a system where the various structures were organs fundamentally *sui generis* in form and arrangement. A similar interpretation has been made by the writer for a monocotyledonous species, *Doryanthes excelsa* (1928).

Both sepals and petals are green at first, and turn bright yellow just before anthesis. The sepals which, in the young stages close over the flower, are only half the length of the expanded petals (Pl. 22. fig. 20 ; Pl. 23. figs. 26 & 27). The general texture of the petals is much lighter than that of the sepals. The striking difference that can be produced by different killing and fixing fluids is seen by comparing the contrast of the petals with the bracts, sepals, and carpels
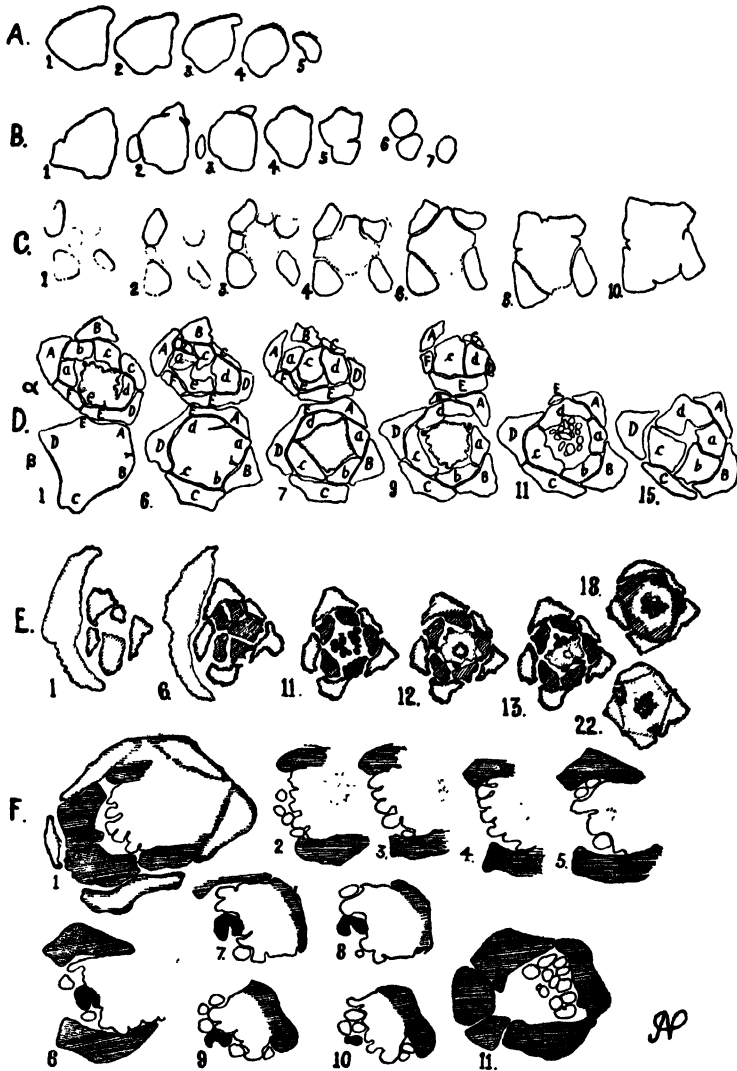
Series of transverse sections through young flowers at various stages. The numbers against the figures refer to the number of the section in the series; in the perianth, outline shading or capital letters indicate the calyx, and complete shading or small letters the corolla. Series A: From base up; only two, possibly three sepal primordia. Series B: From base up; older stage with only three sepals showing clearly, as yet. Series C: From apex down; four sepals and only two petals, all obviously of different ages (tetramerous flower). Series D: Two flowers from base up (α slightly younger than β); showing the beginning of stamens and divergences from the normal number of parts. Flowers were on the same head and spaced as drawn. Series E: From apex down; of the stamens (135° shading), the older are opposite the sepals; central large-celled tissue below depression in the floral apex; bract shown in sections 1 and 6. Series F: Slightly oblique, from base up; carpel (cross-hatched) as a grooved papilla approximately above the large-celled tissue (stippled); not all parts shown in some sections. Sections 6 μ, except in Series D, in which they are 8 μ. A–C, F, × 76; D, E, × 52.

in Pl. 23. fig. 27, with the lack of contrast in Pl. 23. fig. 26 and Pl. 24. fig. 33. The densely staining material is probably some form of gum or mucilage.

The young stamen primordia, when only about seven cells high, already show the beginning of differentiation into filament and anther (text-fig. 4 a). The stamen becomes resolved into a filament which consists only of a tiny vascular bundle surrounded by an epidermis (Pl. 24. fig. 34), and a minute introrse anther which stands erect on the filament (Pl. 24. figs. 29 & 30). The numerous anthers and long coiled filaments are tightly packed in the unexpanded flower, the anthers lying at the distal end being usually at a more advanced
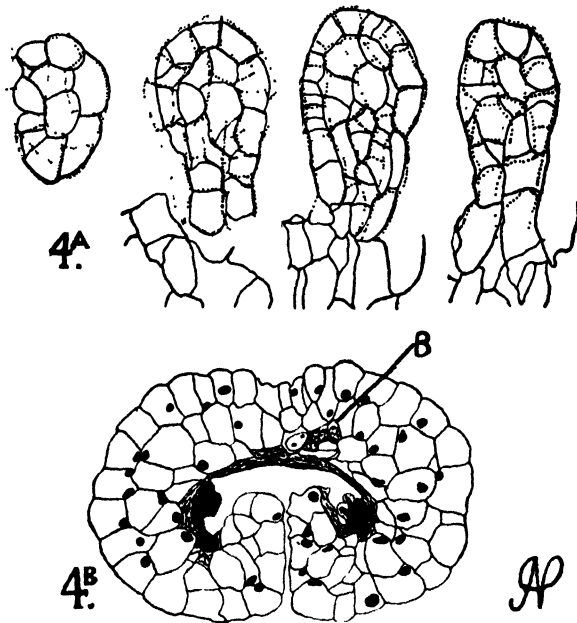
Fig. 4 a.—Consecutive longitudinal sections through a young stamen before formation of archesporia. Continuous lines upper, dotted lines lower focus. 6 μ. × 540.
Fig. 4 b.—Transverse section of young sterile legume showing only midrib primordium, B. Infolded leaf-structure is clearly shown. Note collapse of inner face. × 263.

stage of sporogenesis. In the expanded flower, the filaments are about twice as long as the petals.

The anther is deeply cleft into two main lobes which are each divided by shallow horizontal and vertical constrictions into four sub-lobes (Pl. 24. figs. 29–31), indicating the position of the eight sporangia. The whole product of each sporangium is liberated as a unit—a sixteen-grained pollinium. The two lines of dehiscence are along the vertical constrictions of the main lobes (Pl. 24. figs. 30–31).

The superior gynoecium develops, from the small grooved primordium, as a single carpel in the form of a leaf whose margins turn upwards (towards

the axis) and inwards till they meet to enclose the cavity of the ovary. The tip is extended as the long style, with simple stigma and a canal represented by the region of contact between its two longitudinal limbs (Pl. 24. fig. 31). In older stages this cleft has a densely staining secretion (Pl. 24. fig. 38). The difference in the effect of different fixatives is again shown by comparing the outer two or three layers of the carpels in Pl. 23. figs. 26 & 28 and Pl. 24. figs. 33, 36, & 40, with those in Pl. 23. fig. 27 and Pl. 24. figs. 37–39. The substance concerned seems to be the same as that in the sepals and bracts.

Two oppressed marginal epidermes are clearly present at e in Pl. 24. figs. 33, 36, 38, 40, & 41 (and can also be distinguished in fig. 37), and only at that position in the carpel (see also fig. 39). This means that the carpel is not ontogenetically a hollow cylinder (i.e., does not arise as an annular upgrowth). The vascular supply to the carpel consists of a midrib, B, and two marginal bundles, b, at either side of the line of appressed epidermes (figs. 33, 36, 40, & 41). The midrib passes strongly into the style ; but, even at the time of anthesis, the marginal bundles do not pass into the style (figs. 28 & 37). It will be noticed that it is the midrib (abaxial) side of the carpel that bends outward to provide room for the growing ovules. This makes the style appear to spring from just below the top of the legume at the side towards the axis of the flower-head (i.e. apparently above the appressed margins (Pl. 23. figs. 27 & 28). The twelve (sometimes ten) ovules are in two equal rows along the margins of the legume (Pl. 23. fig. 28 ; Pl. 24. figs. 36 & 40). They are usually completely anatropous when the flower opens, but may be semi-anatropous (Pl. 24. fig. 45). Sometimes they are oblique. The placentation is marginal and apparently adaxial ; but the morphological position cannot be established till the earliest stages are examined.

The placental region of the ovary is covered with thick-walled, unicellular hairs (Pl. 23. fig. 28 ; Pl. 24. figs. 36, 40, & 45), which may, in some young stages, simulate integuments.

One important case of proliferation was found, where a small flower had developed inside another flower. Fig. 35 shows the middle section of a series through the insertion of the small flower on the axis of the large flower. The small flower has not developed beyond the stage of stamen primordia. After making allowances for the obliquity of the sections, and for the fact that the axial tissues beyond the insertion of the carpel of the large flower are still only primordial, it is interpreted that the small flower is the result of continued apical growth of the axis of the large one, and that the carpel of the large flower is therefore lateral. The positive evidence is the flow of tissues, and the junction of the small flower-axis with the carpel-axis distinctly below the limit of infolding of the carpel. The vigorous growth of the carpel has displaced the small flower to one side.

From the evidence brought forward, there seems no alternative to interpreting the gynoecium (legume) of *Acacia Baileyana* as a unitary foliar structure. The details of its development as a single folded organ are similar to those

given by Thompson (1929) for other Leguminosae ; though he interprets the legume as a phylloclade. The details, moreover, are not inconsistent with the figures given for *Acacia suaveolens* by Saunders (1929), though she interprets the carpel as a binary structure.

Thompson regards the legume of *Pisum sativum* and other Leguminosae as being not a foliar organ, because it was invariably found to be initiated as an erect terminal column ; and because the secondary vasculation is not leaf-like, as it does not spread from the dominant midrib.

The proving of an organ to be terminal, or lateral to a suppressed apex would require a detailed study of tissue-flow in longitudinal sections of the earliest stages. No such figures are given by Thompson ; but he says ' The question then arises whether such delayed apices can be demonstrated, but it may here be noted that at no point in the early stages of the gynoecium has any indication of such apices been found '. The requisite stages were not available for examination in the present Study ; but there is recorded one case of proliferation (Pl. 24. fig. 35) which I interpret as the continued growth of the usually suppressed apex, so that the legume becomes definitely inferior, though, by its greater growth, overtopping the small arrested flower. In this case the legume would be infolded towards the axis, the condition expected if it were really foliar.

The carpel of *A. Baileyana* is so reduced that even by the time of fertilization there is no sign of the secondary vasculation ; and older carpels have not yet been examined. But if the legume is an axial structure (' phylloclade '), as suggested by Thompson, would not the three bundles organized by that time be of more equal status than is indicated by the omission of the marginal ones in the sterile legumes of *A. Baileyana* ? Moreover, would not the marginal bundles extend into the style, contrary to their ending before it, as described here for *A. Baileyana* and by Thompson for other Leguminosae ?

Saunders (1925), by the theory of Carpel Polymorphism, makes the typical legume to consist of two carpels, one fertile and one sterile. In a later communication (1929) she brings *A. suaveolens* and *A. longifolia* under the theory, but leaves us to speculate just where their legume is divided. However, all gradations between completely fertile and completely sterile legumes are manifested in *A. Baileyana*, in such a manner that the difference between fertility and sterility could not lie in the presence or absence of the fertile one of two carpels. So the same essential structure must be found in the fertile legume as in the sterile one which is undoubtedly a single carpel. Hence the fertile legume of *A. Baileyana* must be a unitary structure. In it, the marginal bundles develop only to the same degree as the fertility whose needs they serve, and no further than the region of fertility (viz. not into the style). Therefore, they could not be primary structures such as the twin bundles of a fertile ' semi-solid carpel '. Moreover, it seems reasonable to give more weight to detailed histological evidence from the initial stages than to the plan of vasculation (much of it probably of secondary origin and a physiological response)

shown in the developing fruit. Parkin (1926) also considers that to make a morphological division of a fruit on the basis of its vasculation is unsound, because of the secondary nature of many of its bundles.

Guard (1931) describes the legume of *Soja max* arising as a folded foliar structure. A similar interpretation is retained for the legume of *A. Baileyana* by the writer.

STERILITY

Sterility may set in at any stage in any or all of the reproductive organs, and is variable in its incidence. Neither complete sterility nor complete fertility of a flower is frequent. In any one flower, sterility in the gynoecium alone is very frequent ; but in the androecium alone it is infrequent. Flower-heads with all gynoecia sterile are frequent ; but those with all androecia sterile are infrequent. Sometimes a whole flower having ceased growth at the archesporial stage has been observed.

Stamens that have produced no sporogenous tissue, while the rest of the flower is well developed, have not been found. A typical case of androecial sterility due to degeneration during meiosis, with collapse of the sporogenous tissue (S) is shown in Pl. 24. fig. 42. Though most microsporangia have been fatally affected, a very few may produce spores, and such may have abnormal meioses, as in the mother-cell at 1 in fig. 42, shown also in fig. 42 *a*. (This spindle and that shown in Pl. 24. fig. 48 are in different flowers on the one flower-head.) This condition shows the possibility of a pollen-grain being occasionally formed with an aberrant number of chromosomes.

There is a connection between sterility and the absence of the deeply staining substance in the outer layers of the carpel (legume). Excluding material fixed in the mercuric chloride fixative (of 99 carpels examined), 51 had the deeply staining substance fully present and 48 had varying degrees of its absence. In all but one of those having it fully, the ovules had reached full size. Of the other 48 : 28 had never begun to form ovules, 15 had ovules that had suffered early degeneration, and 5 had normal ovules which, being only at the megaspore stage, had ample opportunity left for degenerating. The less of the staining substance present, the smaller is the carpel and the earlier the degeneration of the ovule.

The completely sterile carpel remains a small leaf-like structure, usually loosely coiled longitudinally, but sometimes with its margins meeting. The midrib is represented by a plerome, but the marginal bundles are absent (text-fig. 4 *b* ; Pl. 24. fig. 34).

Sterility may set in at any stage in megaspore or embryo-sac formation.

There are several distinct modes of sterility. The first concerns the whole flower, which remains ill-developed. Secondly, there is sterility of the parts (stamens or carpels), in which case no archesporia are laid down in the stamens or ovules in the carpels, yet the parts persist in a recognizable and undamaged condition. Thirdly, there is sterility in the product of the archesporium at

some time of development. And, fourthly, there is sterility in the product of the sporangium. Examples of all modes, except sterility of the stamen, have been observed. These modes may be due to different inherent factors or to different intensities of one factor.

The sterility in *A. Baileyana* seems to be rather incidental and without direction, compared with the definite trend of advancing sterility described by Thompson (1924 and 1925) in the Amherstieae and Cassieae sections of the Caesalpinioid Leguminosae. No transition of stamens into petals, nor any suggestion that the legume was residual of a branched gynophore were observed (*cf.* Thompson, 1929). As a matter of fact, there are many functionally unisexual flowers, mostly male ; but the androecium is, in general, far from approaching functional elimination.

SPORANGIAL STRUCTURES

MICROSPORANGIA.

The eight microsporangia arise separately ; but whether they are morphologically superficial or embedded has not yet been determined. The slight evidence already found suggests that there is a single hypodermal archesporial cell for each sporangium. The tissues in the anther are so extremely reduced that it is difficult to assign them, especially in view of the absence of preparations of undegenerated early stages.

In a flower whose anthers were beginning to degenerate, the primary sporogenous cells, sometimes divided, were seen in the sub-hypodermal position. Some, at least, of the hypodermal cells in these anthers would be primary parietal cells. There is no indication of the origin of the tapetum, not even by observation of the lines of cleavage in the adult tissue.

The maximum development of the parietal tissue is two or three layers, and is attained by the time of meiosis. Between transverse or longitudinal pairs of sporogenous groups there are only two or three layers. The outer layer (hypodermal) becomes very much broader than the other layers (except under the longitudinal depression) about the time of synapsis, the difference increasing till the microspores have been organized. These points are shown in Pl. **24.** figs. 31 & 46 and Pl. **25.** figs. 50–57.

The endothecial thickening, confined to the lateral and inner walls of the hypodermal layer at the sides of the anther-lobes (Pl. **24.** fig. 31), is laid down about the time of the division of the microspore-nucleus. The result is strikingly suggestive of the annulus of a leptosporangiate fern sporangium. Differential staining with safranin and light green gives red thickenings on green walls, allowing the photo shown in fig. 31 to be taken.

Besides the tapetum proper, the one or two inner layers of the parietal tissue become used up during sporogenesis. These layers are regarded as forming an ' outer tapetum '. Each sporangium has its own tapetum proper ; but between sporangia the outer tapetum is shared.

The cells of the tapetum proper are larger than those of the inner parietal layers (outer tapetum) ; their cytoplasm is very dense and granular ; and the nuclei are relatively large, often with chromosomes organized, and sometimes rivalling the nuclei of the pollen mother-cells in size and appearance. During the formation of the exine on the spores, a form of interrupted thickening similar in staining reactions to the exine is laid down on the inner face of the tapetum proper ; it remains a conspicuous feature of the dehisced anther (Pl. 24. figs. 30 & 31 ; Pl. 25. fig. 55).

The outer tapetum is used up during the division of the exine, and the inner tapetum during the division of the microspore nucleus. The tapetal features are to be seen in Pl. 24. figs. 46 & 48 and Pl. 25. figs. 50, 51, 53, & 57.

Rosanoff (1865) describes various aspects of the anther in several species of *Acacia*, the disposition of the tissues being very similar to that in *A. Baileyana*. An exception is the persistence of the inner parietal layers of *A. verticillata*. He does not figure any stage before the first division of the primary sporogenous cell. Engler (1876) only figures a cleared anther of *A. cultriformis*, which is remarkably similar to Pl. 24. fig. 30 of this paper. He gives details of the development of the tissues in *Albizzia lophantha*, which are slightly larger than, but similar to, those of *Acacia Baileyana*, definitely manifesting eight separate archesporial cells.

MEGASPORANGIA.

The megasporangium is borne sunken in a receptacle (nucellus) which arises at the margin of the sporophyll (carpel). The archesporium is hypodermal and usually unicellular. One ovule was seen having two mother-cells in synapsis, with crushed cells between them, and with distinct parietal tissues (Pl. 24. figs. 43 & 44), suggesting two archesporial cells. The disposition of these two mother-cells in one ovule suggests a stage in the reduction of the many-celled archesporium of the Rosaceae.

The archesporial cell divides to a primary sporogenous cell and a primary parietal cell (text-fig. 8). There is no definite tapetal tissue formed, its function being carried out by the crushing of adjacent cells of the receptacle (nucellus) and parietal tissue (nucellar cap).

A discussion and explanation of the use of the terms ' receptacle ', ' embedded sporangium ', ' parietal tissue ', in connection with the ovule will be found in an earlier paper by the writer (1928).

The amount of parietal tissue is variable, from two to three layers of two or three cells each, capping the mother-cell or spores (text-figs. 8–16 ; Pl. 25. fig. 58). Sometimes it is difficult to distinguish the tissue clearly ; sometimes it is quite regular and distinct. The little crushing that does take place is restored by cell-divisions, for two or three layers cap the mature embryo-sac (Pl. 24. fig. 45).

The receptacle is bent at the junction of the funiculus and chalaza to angles of from 90° to nearly 180°. It develops only vestigial integuments which arise

about the time of megaspore formation and, at fertilization, are still only minute ridges round the chalaza (Pl. 24. fig. 45). The outer integument does not, as usual, make the complete circle. The ovule is virtually naked.

The ovule is very small. The increase in size from the time of synapsis is due to the swelling of the embryo-sac ; and not to growth in number of the cells of the receptacle, which remains two or three cells thick at the sides of the sac and increases only from six cells to eight cells across the chalaza. The funiculus grows similarly, and is in such a reduced state that no vascular tissue is organized in it by the time of fertilization.

A deceptive feature is the great size of some of the nuclei of the nucellus ; they may be even larger than spore-nuclei.

There is no tapetum proper. Very little crushing of adjacent cells by the enlarging mother-cell or embryo-sac takes place to serve the tapetal function.

Guignard (1881) describes the development of the ovule in several species of *Acacia*, with general similarity to that given here, but with several exceptions. He describes multiplication in the epidermis of some species, a phenomenon absent from *A. Baileyana*. More important still, he describes the beginning of the inner integument about the time of the formation of the megaspores, in *A. retinodes* with the beginning of the outer integument soon afterwards. The integuments of *A. exudans* are described as reaching the summit of the nucellus. This integumental feature is entirely different from that in *A. Baileyana*, where the integuments, arising about the same time as those described by Guignard, remain vestigial. The time of origin of the integuments is late, compared with the general statement of Coulter and Chamberlain (1903), and is therefore regarded as a step towards elimination, even where the integuments are fully formed. Another difference is that, in some of the species described by Guignard the embryo-sac crushes all of the receptacle and parietal tissue at the side of and above itself.

SPOROGENESIS

MICROSPORE.

The primary sporogenous cell divides twice at right angles to form the four mother-cells lying in one plane parallel to the long axis of the anther (Pl. 24. fig. 46 ; Pl. 25. figs. 51 & 57). (The completion of the first division has been seen only in degenerating anthers.) The process of meiosis is carried out rapidly, for prophase of heterotypic division and completed tetrads can be found in one and the same anther (*cf.* also fig. 51). But the four mother-cells, or their derivatives, in any one sporangium are always at the same stage of development.

The outer walls of the mother-cells become increasingly thicker than the inner walls (text-figs. 5 & 7 ; Pl. 25. figs. 57, 59, & 60) as meiosis proceeds. The cytoplasm of the resting mother-cells is dense, but loosely reticulate. A feature of these cells is the large size of the nucleus, which is half the linear dimensions

of the cell, before the prophase of meiosis starts. The nucleolus, set in a clear area of the nucleus, is also comparatively large and, with some fixatives, shows a heavy membrane and a dark inclusion.

The cytological details are followed only as they have a general bearing on the course of morphology or indicate lines of further inquiry.

At synapsis, the mother-cell cytoplasm has become finely reticulate and very dense ; the cell increases slightly and the nucleus greatly in volume (Pl. 24. fig. 46 ; Pl. 25. figs. 50 & 51). The appearance known as synizesis is plentiful (fig. 46), and may occur in the same flower with normal pachytene. A curious feature is the occurrence of certain twin bodies on the edge of the cytoplasm at diakinesis, one pair to each cell (Pl. 25. fig. 59). No evidence of their origin has been seen.

The nucleolus, apparently unchanged, persists till diakinesis and then suddenly disappears. It offers another example of the different effect of different fixatives. Figs. 46 & 57 (Pl. 24 & 25), showing light nucleolus, are from material fixed in fluid D : figs. 50 & 59 (Pl. 25) from material in fluid C, and fig. 51 from material in fluid A show dark nucleolus. The difference would seem to be due to the absence or presence of chromic acid or of acetic acid.

The pachytene thread, well distributed throughout the nucleus, shows the chromomeres very plainly (Pl. 25. fig. 50). Occasionally it is gathered into a bouquet of loops (Pl. 24. fig. 47), resembling the ' brochonema ' described by Latter (1926) in Lathyrus odoratus. The pachytene thread has been followed for considerable lengths and is lost, either because it passes out of the section or is too tangled ; so that there is still the possibility that a cytological inquiry may show it to be continuous. At early diakinesis (Pl. 25. fig. 59) the chromosomes have a beaded appearance. The members of each pair certainly correspond with one another ; and, making allowances for the curves in many of the chromosomes, there is strong reason for expecting that a careful cytological inquiry would reveal the existence of definite types in length and configuration. This is still suggested by the much more condensed condition at early metaphase (Pl. 25. fig. 60). There is the usual extreme contraction of the gemini at the equatorial plate stage (Pl. 24. fig. 48 ; Pl. 25. fig. 51). The extreme separation of some of the ' beads ' from the remainder of some chromosomes in diakinesis suggests the presence of trabants, of which there are further indications at interkinesis (text-fig. 5) and homotypic anaphase (Pl. 25. fig. 61).

The spindle first appears with at least three poles, but finally becomes bipolar (Pl. 24. fig. 48 ; Pl. 25. figs. 50 & 51). With no constant orientation of the spindles, the daughter-nuclei are variously placed in the pollinium-mother (text-figs. 5 & 6 ; Pl. 24. fig. 49).

No walls are formed at the end of the heterotypic division, but fibres appear in the cytoplasm, perpendicularly to the walls of the mother-cells (fig. 49). At interkinesis the chromosomes appear split, and retain a considerable degree of their condensation (text-fig. 5 ; Pl. 24. fig. 49). Trabants are indicated. The nucleolus reappears during interkinesis, only to disappear before homotypic metaphase.
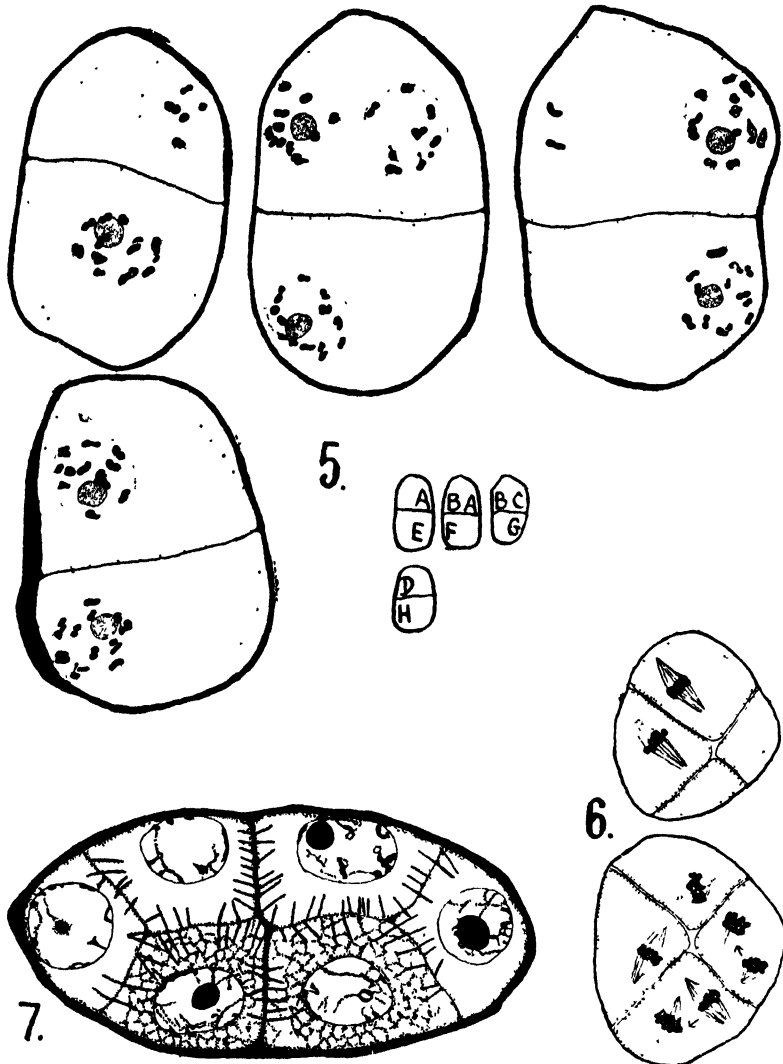
Fig. 5.—Consecutive sections through a pollinium-mother at interkinesis, parallel to one partition-wall and passing from front to back. Thirteen chromosomes in each of the uncut nuclei C, D, E, F, G and the cut ones A, B ; number in H is indeterminable (see small drawings for positions of nuclei). The split in the chromosomes and their occasional superposition makes the identity difficult to show. Trabants are indicated. × 1,800.

Fig. 6.—Two consecutive sections of a pollinium-mother showing the irregular orientation of the homotypic spindles. Dotted fibres indicate the lower end of the spindle. × 758.

Fig. 7.—Median section (edge view) of a completed pollinium before germination of the microspores. Only one plane of focus shown in the drawing. Zonation of the cytoplasm and fibres perpendicular to the inner walls. Drawing not completed. × 1,770.

The bipolar homotypic spindles are formed in random directions (text-fig. 6), and the chromosomes at anaphase show trabants and suggest individuality (Pl. **25**. fig. 61). At telophase, fibres appear between all four tetrahedrally arranged nuclei in any one mother-cell, and walls cut off the four spores simultaneously (text-figs. 6 & 7 ; Pl. **25**. fig. 56 &c.).

The spores thus being constituted, fibres also appear against the internal walls of the mother-cells, and persist for some time during the thickening of the walls of the spores (text-fig. 7). The thickening is very heavy at the angles. The cytoplasm becomes loosely vacuolate, more largely so along the inner walls. The nuclei have a conspicuous nucleolus and a loose knotted chromatin condition (text-fig. 7 ; Pl. **25**. fig. 56).

The final disposition of the spores in the mother-cell is that of a tetrahedron slightly distorted, so that two of the faces are at right angles (the angle between the common walls of the mother-cells). In flat surface-view, twelve spores can be seen, while, in sections, from one to twelve can be seen according to the level and inclination of the plane of section (Pl. **24**. fig. 32 and Pl. **25**. figs. 55, 56, &c.). The whole sixteen spores produced in one sporangium are liberated as a unit, a pollinium.

The simultaneous formation of the microspores is a typical dicotyledonous condition (Schürhoff, 1926). The general course of microspore formation given here is similar to that described by Engler (1876), as far as the two descriptions go. Rosanoff (1865) describes binucleate conditions in the primary sporogenous cell and its daughter-cells for *Acacia paradoxa* and in the primary sporogenous cell for *A. verticillata*. No such condition has been identified in *A. Baileyana* ; and probably it is only apparent in the other two species because the wall separating the nuclei was not seen because of its obliquity or the density of the cytoplasm.

The earlier investigators spoke of ' sixteen-celled ' pollen-grains. Engler was the first to recognize the structures as groups of sixteen pollen-grains, the entire products of sporangia. Such structures, since called ' pollinia ', may have multiples of four pollen-grains, according to the number of mother-cells concerned. Engler found sixteen to be the most frequent number for Acacias ; though he found twelve in *A. decipiens*, *A. pulchella*, *A. nigricans*, and *A. pentadenia*, eight in *A. paradoxa* DC. (=*undulata* W.) and *A. cordifolia*.

MEGASPORE.

The usually single primary sporogenous cell functions as the mother-cell, the cytoplasm of which in the resting condition is more finely vacuolate than that of the microspore mother-cell. The large nucleolus has the usual loose knotted reticulum.

In attaining to synapsis, the length of the mother-cell is doubled, and its breadth and the diameter of the nucleus are increased by nearly one-half. The early stages of meiosis are similar to those in the microspore mother-cell. Both the well-distributed pachytene thread and the ' synizetic ' condition

are found in the same carpel, and even in the same ovule in the one case where there were two mother-cells (Pl. 24. figs. 43 & 44). This case shows how sensitive that stage is to the fixative, since only one of the two so close together shows collapse. Or does it mean that the synizetic knot is a valid condition, for otherwise the cells look equally healthy ?

The heterotypic spindle was not seen, but a very late diakinesis or very early metaphase without spindle-fibres was found, showing a recognizable grouping of chromosomes which appear to be of different configurations. The group was too intermixed at the centre to allow of the precise unravelling of the chromosomes in that region (Pl. 25. fig. 62).

So far as can be inferred from the evidence, it seems that a wall is laid down at the end of the heterotypic division. As the homotypic division does not always take place in both daughter-cells, it is not unusual to see only three megaspores (text-fig. 13). The three or four spores are disposed in an axial row (text-figs. 12–16).

Usually all except one of the spores soon begins to break down. Two exceptions were seen. One very much degenerated ovule had two embryo-sacs which were recognised by the ' beaks ' on the synergids, and are interpreted as being the result of the functioning of two spores. This is supported by the other exception, where two megaspores were contending ; the wall separating them having been oblique allowed the lower one to have a chance of developing (text-fig. 14). There is no set position for the functional spore, which may be either distal (more frequent—text-figs. 12, 13, & 15) or chalazal (text-fig. 16).

The functional spore has a finely vacuolate cytoplasm which later becomes more largely vacuolate. The nucleus has a loose chromatin thread with aggregations and a very prominent nucleolus (text-figs. 12–16).

The formation of the megaspores appears to be succedaneous, as recorded for several other species by Guignard. He finds three equal spores at first in some species and four in others ; and says that the chalazal spore is the one that functions, except in *A. albida*, in which the second spore functions. In *A. Baileyana* it has been found that three or four spores may be formed and that either the distal or chalazal spore may develop. In *A. exudans*, Guignard found the vertical division of all the non-functional spores before the functional one began to enlarge. This raises the question whether the approach to vertical division found in *A. Baileyana* (text-fig. 14) was a division of a spore or was the homotypic division in spore-formation. The apparent attempt of both cells to function lends support to the latter interpretation.

SIGNIFICANCE OF MEIOSIS.

The occasional failure of one daughter-cell to divide after the heterotype division in megasporogenesis raises a question in connection with the recent chiasmatype theory of meiosis (see Darlington, 1931). According to that theory, at heterotypic anaphase there is a separation of *pairs* of chromatids
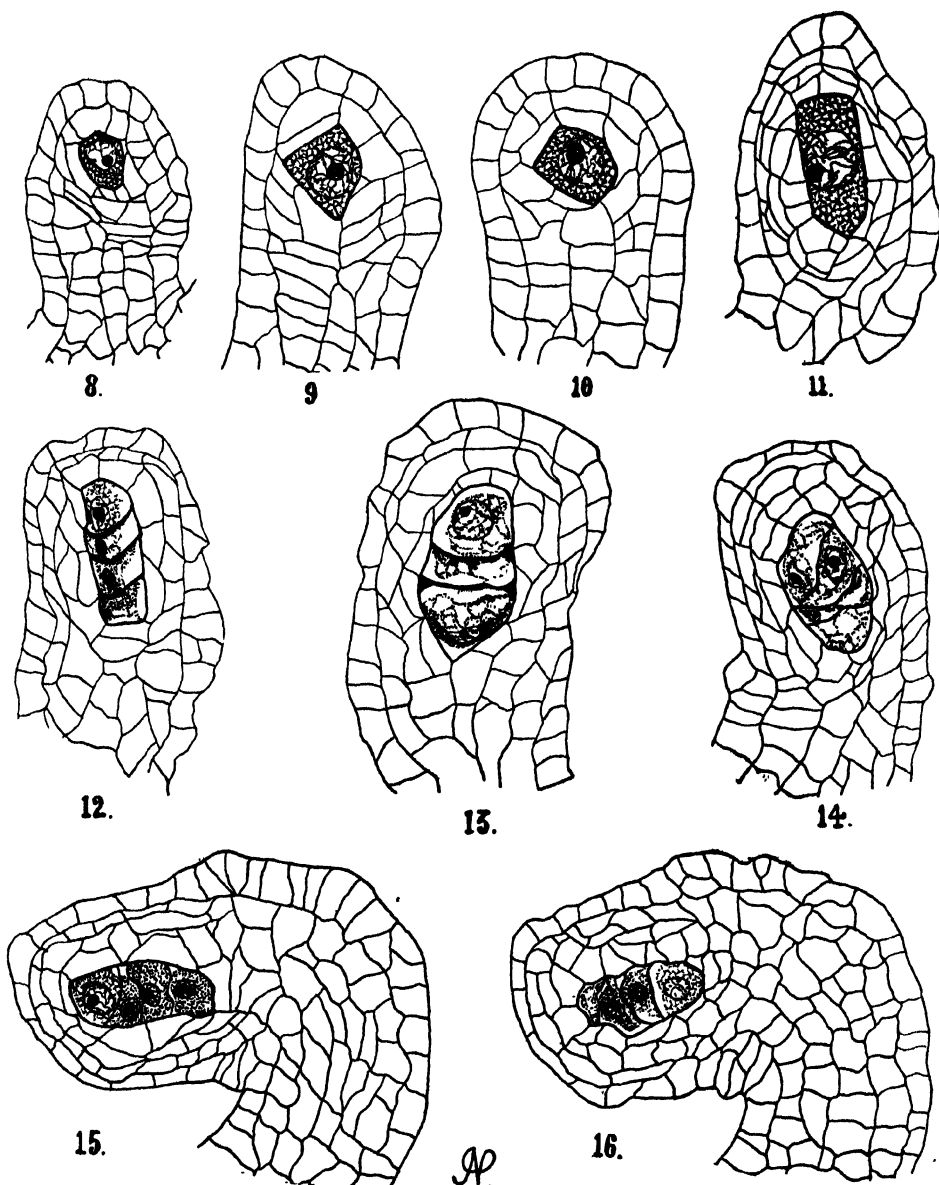
Figs. 8–16.—Longitudinal sections of young ovules showing stages in the formation of the megaspores. 8, primary sporogenous cell (protoplasm shown) below primary parietal cell. 9–11, mother-cell from resting to pachytene conditions, with divisions in the parietal tissue capping it. 12, 14–16, four megaspores showing distal (12, 15) or chalazal (16) spore-functioning, and the two upper ones in 14 contending. 13 shows only three spores, with the distal one functioning. Note the regularity of the parietal tissue over the spores in some cases, and the very faint beginnings of the vestigial integuments just below the level of the spores. 8, ×534; 9, 10, ×680; 11, ×597; 12, ×694; 14–16, × 600.

to opposite poles, the chromatids of each separated pair being slightly different from one another ; then, at homotypic anaphase, there is a separation of *single* chromatids to opposite poles. This may be shown in a diagram as follows :—
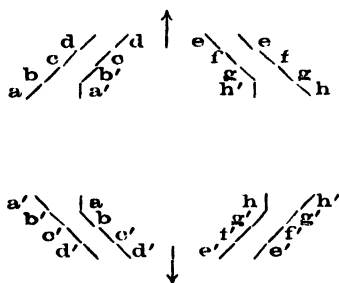
Separation of pairs of chroma-
tids at heterotypic anaphase.
$2n=4$.
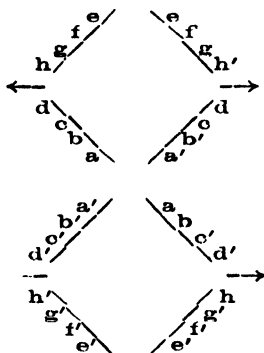
Separation of single chroma-
tids at homotypic anaphase.
$2n=4$.

The four spore-nuclei would each have two chromatids as below :—

abcd	a'b'cd	a'b'c'd'	abc'd'
efgh	efgh'	e'f'g'h'	e'f'g'h

If division does not occur in the top daughter-cell, for instance, then there are two spores with two chromatids each, and one ' spore ' with four chromatids, the nuclear content being :—

abcd, a'b'cd	a'b'c'd'	abc'd'
efgh, efgh'	e'f'g'h'	e'f'g'h

The significance of this lies in what happens in the first division of the nucleus of a functional spore which is an undivided heterotypic daughter-cell. If that division is a separation of single chromatids, the probabilities for the chromatin-content of the egg-cell remain unaltered ; but the ratio of zygotic and endosperm characters would be materially affected, compared with the probabilities when a normal spore functions. If in that division there is not a separation of single chromatids, but the pairs function as chromosomes, it would lead to many genetical anomalies, if fertilization were not rendered impossible because of chromosomes which were internally ' heterogeneous '. Whatever be the genetical possibilities of the results of the delaying or suppression of the homotypic division, there should be an ascertainable cytological difference between the two possible first divisions in the megaspore as outlined above.

The split in the chromosomes at early interkinesis (anther) is suggestive of that found by Gates and Sheffield (1929) in *Oenothera rubricalyx*, and may be an expression of the lack of complete similarity of the chromatids postulated in the chiasmatype theory. This phenomenon should be of use in considering the nature of the first division of a functional spore which is an undivided heterotypic daughter-cell.

CHRONOLOGY AND SYNCHRONOLOGY

The flower-buds are started at the end of the previous season. In the natural habitat of the Cootamundra district, the flowering season is in early September ; but trees cultivated in the lower altitude and warmer climate of Sydney flower in late July (end of winter). It is probable that the flowers pass the summer, autumn, and early winter in a dormant condition at a fairly advanced stage of sporogenesis. In the development of flowers from primordial stages just before the main crop comes into bloom there is a great incidence of degeneration, particularly at the young stages.

For the sake of clearness, reference to the synchrony of the different lines of development has been reserved for separate description here.

Stages may differ from flower to flower on the one head, even within one flower ; and they occur so rapidly at some periods that there is a discrepancy between the stages within one another. It is therefore impossible to give an ordered and accurate table of synchronology.

The spores are formed by the time the flower-head is half size. The stamens begin to enlarge at the top (still very small) when the carpel is a small, vertically grooved papilla. Meiosis in the anther, even with completed tetrads, is found in the same flower as the primary megasporogenous cell. Meiosis occurs in the ovules when the microspore exine is being deposited. By the time the megaspores are formed, the pollen is binucleate. The vestigial integuments appear about the time of megaspore-formation. In the anther the endothecium is laid down before the division of the microspore-nucleus ; and the tapetum proper is used up about the time of that division.

CHROMOSOME NUMBER AND TYPES

The haploid number of chromosomes is thirteen. This number has been counted in various stages of meiosis in the anther. Thirteen pairs were seen at diakinesis (Pl. 25. fig. 59) and heterotypic metaphase (Pl. 25. fig. 60) ; thirteen chromosomes in heterotypic anaphase groups (Pl. 25. figs. 52–54 a), in early interkinesis (text-fig. 5), and in homotypic anaphase groups (Pl. 25. fig. 61). An examination of the sizes of the chromosomes in these figures, especially 59 and 61 shows that there are considerable differences, which may be expressed as nine or ten large and four or three small, some with trabants.

Ghimpu (1929 a, 1929 b) has studied the chromosomes in the root-tips of thirteen species and varieties of *Acacia*. He has found the diploid number in six Australian species (*A. cyanophylla, A. dealbata, A. podalyraefolia, A. saligna, A. decurrens,* and *A. longifolia*) to be twenty-six. In the silhouette figure he gives of a metaphase of *A. cyanophylla* three or four pairs of chromosomes appear to be definitely shorter than the remainder, suggesting a similar condition to that shown in *A. Baileyana*. In six Asian and African species (*A. arabica, A. nilotica, A. horrida, A. Farnesiana, A. eburnea, A. scorpioides* var. *pubescens*) he found both about 52 and 104 chromosomes in different cells in the same root-tip ; and in a seventh, *A. scorpioides* var. *astringens*, there were

nnclei with 52, 104, and 208 chromosomes. The six endemic Australian species have normal mitosis ; but the other seven have unusual features in it. *A. Farnesiana* has a very wide indigenous distribution in western, north-central, and north-eastern Australia, and perhaps south tropical Africa (Bentham, 1875). In view of its different chromosomes number—twice that of the other six Australian species recorded—and its abnormal mitosis, it is interesting to note that it is the only indigenous Australian species to be found elsewhere. It will therefore be of considerable importance from the evolutionary point of view, unless it be shown to have been introduced recently.

Thirteen as a basic chromosome number is of very recent discovery in the Leguminosae. Gaiser (1930 *a* & 1930 *b*), in the list of chromosome numbers found up to the end of the year 1929, records almost entirely seven or low multiples of six and eight for the haploid numbers. Of the exceptions, those to be noted here are the *Acacia* species given above with a basic number of thirteen, and *Cassia occidentalis* with a haploid number of thirteen. This suggests an approximation to tetraploidy based on the six and seven numbers.

Tischler (1922) speaks of trabants which ' unter den somatischen Chromosomen kleine " eigentlich " überzählige, welche an grössere angehängt erscheinend in den allotypen Mitosen offenbar völlig mit ihnen verschmolzen sind '. The strong suggestion that in *A. Baileyana* the trabants are discernible at some stages of the allotypic mitoses (meiosis) is of importance. This question, particularly the stages of diakinesis (Pl. **25.** fig. 59), interkinesis (text-fig. 5), and homotypic anaphase (Pl. **25.** fig. 61), will be closely examined in a projected study of the cytology of *A. Baileyana*—for a record of trabants in meiosis would be of much interest.

These facts of chromosome number and configuration point to a great field of cytological inquiry, which will be of considerable value in elucidating the problem of the species among the Australian members of the genus *Acacia*.

CONCLUSION

The discussion of the position of *A. Baileyana* in the genus will be reserved till the completion of the life-history. Considered apart from its relation to the larger inquiry, the part of the life-history of *Acacia Baileyana* described provides a number of interesting phenomena, some of which will prove to be of considerable importance. The following are considered to be the more important facts established :—

1. The occurrence of the species in an area of the conjunction of three elements of habitat.

2. The clear manifestation of different effects of fixatives, shown in the floral members and in the nucleoli of the sporogenous tissue.

3. The nature of the flower-head as an example of the maximum condensation of a spike.

4. The legume as a unitary foliar structure.

5. The record of a flower produced within a flower, by growth of the floral axis after the legume had been formed.

6. The varying degrees and times of the onset of sterility.

7. The ovule is naked, the integuments being barely discernible.

8. The case of two mother-cells in one ovule.

9. The delaying or suppression of the homotypic division occasionally in one of the heterotypic daughter-cells in the ovule (three megaspores).

10. The variable position of the functional megaspore.

11. The nature and development of the sixteen-grained pollinium.

12. The simultaneous microspore formation.

13. The existence of chromosome types, probably nine or ten long and four or three short, some with trabants.

14. The strong suggestion of trabants during early stages of meiosis.

15. The haploid number of chromosomes is thirteen.

The work upon which this paper is based was begun while the writer was, for three months, a Research Student in the Department of Botany at the University of Sydney. The major portion of the work has been carried out in the Department of Botany at King's College, London. The thanks of the writer are due to Professor R. Ruggles Gates, F.R.S., for his interest and advice during the course of the work. He would also express thanks to his fellow-students in the Cytological Laboratory for their assistance in confirming observations.

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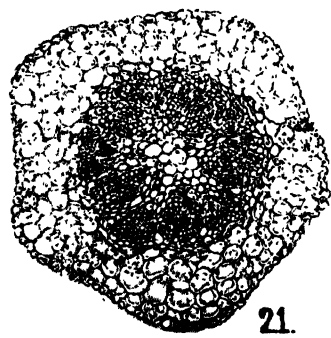
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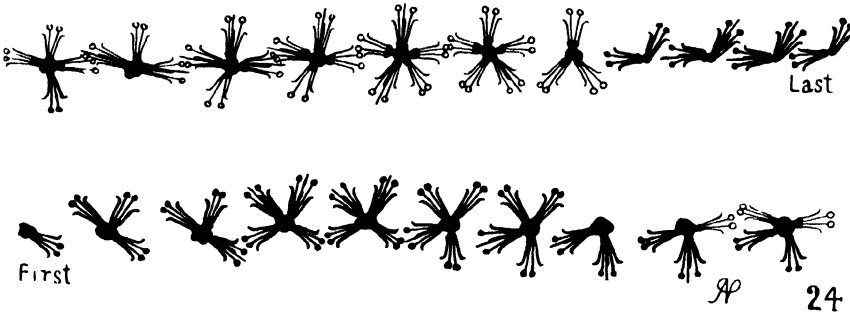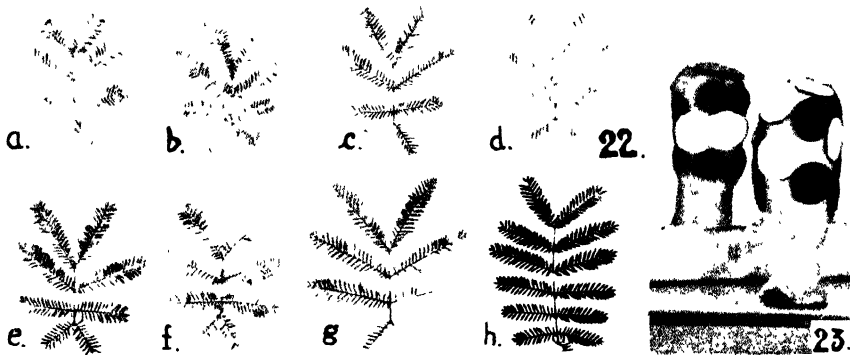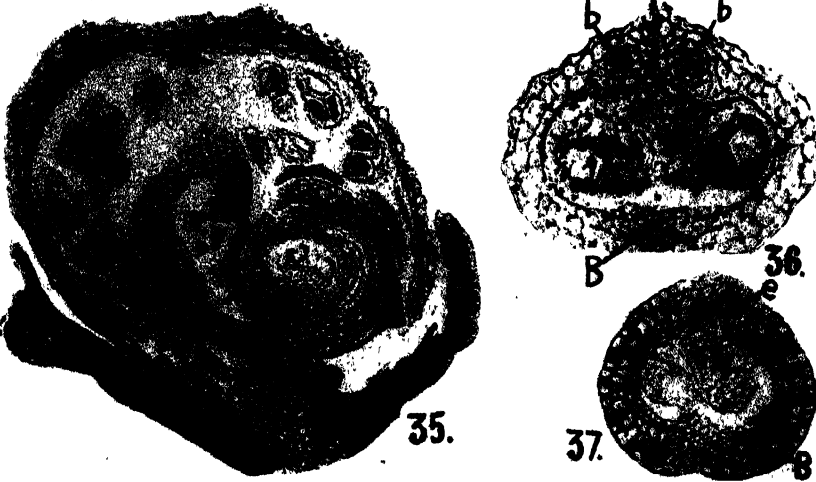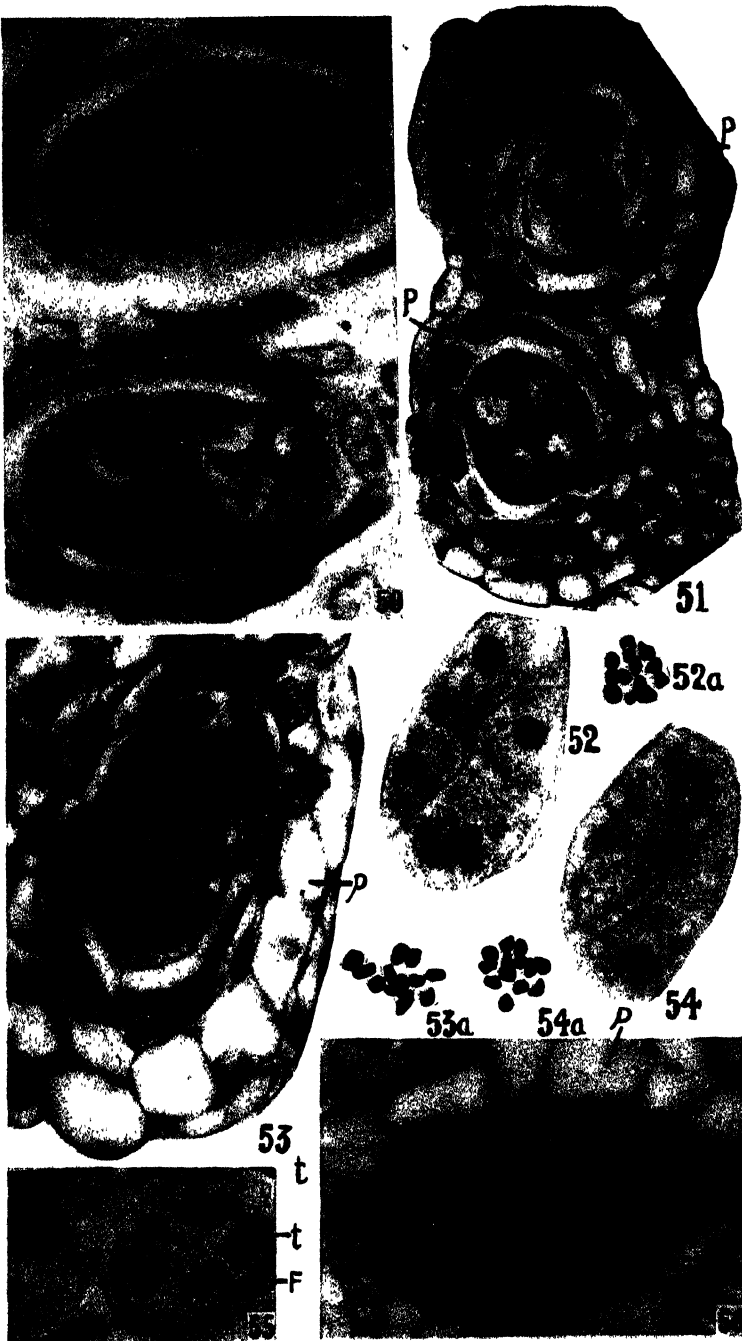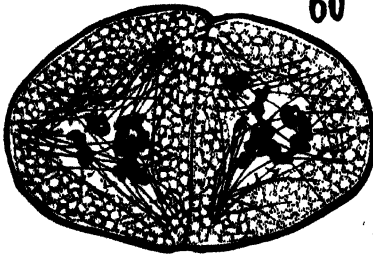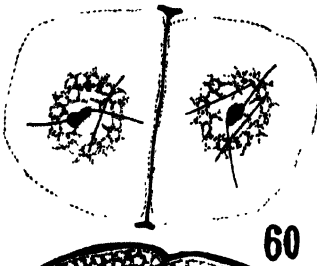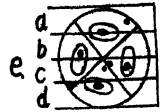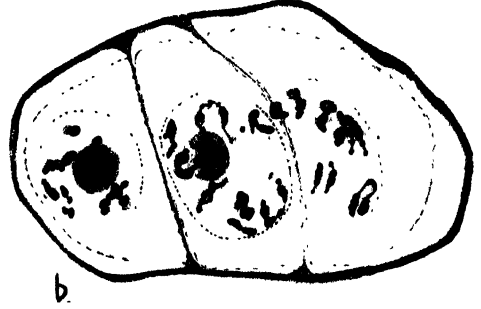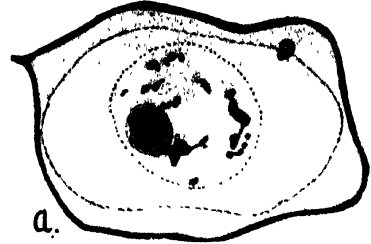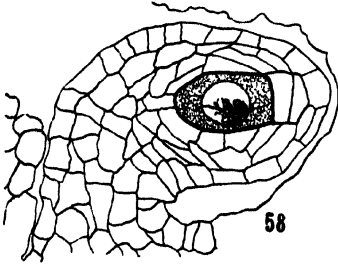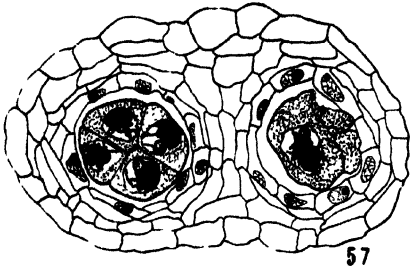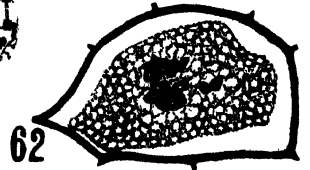
ACACIA BAILEYANA

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EXPLANATION OF THE PLATES.

[All drawings, text-figs. 1–16, and figs. 24, 42 *a*, 52 *a*, 53 *a*, 54 *a*, 57–62 in the Plates are the work of the writer, and except text-figs. 1 & 2, and fig. 24 (Pl. 23) were done with the aid of a camera lucida. The photography is the work of the writer, except as follows :—Fig. 17 is by Mr. H. G. Gooch of the Geology Dept., University of Sydney ; the negatives and prints for Figs. 21 (original for), 24, 29, 32, 35, the negatives for figs. 22, 47, 50, and the prints for figs. 18, 19, 30, 38, 43, 44 are the work of Mr. C. S. Semmens of the Botany Dept., King's College, London. I wish to express my thanks to these gentlemen for their good services.

The numbers of the figures (17–62) in the Plates are consecutive with the numbers of the figures (1–16) in the text.]

PLATE 22.

Fig. 17. *Acacia Baileyana* in cultivation at Sydney. The white stick is one metre. Notice the young racemes and glaucous foliage.

Figs. 18, 19. Two twigs showing 2/5 phyllotaxy. 18 is clockwise, 19 anti-clockwise. Of the raceme axes (flower-heads fallen) on 18, the lowest is clockwise, the centre anti-clockwise, and the upper clockwise. × 1/3 approx.

Fig. 20. Longitudinal section of a young flower showing large-celled central tissue, perianth members on the side of the cylindrical thalamus, and the tip of the subtending bract overlapping the ' heel ' of a higher bract. × 160.

Fig. 21. Transverse section of the pedicle of a flower-head showing five-rayed medulla. × 96 approx.

<div align="center">PLATE 23.</div>

Fig. 22. Typical leaves from eight trees labelled *Acacia Baileyana* at Kew Gardens. Some pinnules have fallen from *f* and *g*, and one of the lowest pinnae from *c* and *h*. For explanation, see text.   × 3/8 approx.

Fig. 23. Model of flower-head, with reflection in mirror. Whorls are alternately black and white. For explanation, see text.

Fig. 24. Series of semi-diagrammatic transverse sections of a flower-head showing the grouping of the flowers in ' whorls ', possibly each whorl a spiral. Series from the base up. Lowest whorl drawn thickly, next drawn thinly, third (only two flowers) drawn thickly. Flowers indicated only where sections pass through the place of insertion on the axis. The figure was made by copying the sections of the flower-head axis from a photo of the preparation. × 4 approx.

Fig. 25. Longitudinal section of young flower-head, showing large-celled tissue in axis and thalamus, the enclosing bracts, and the sepal primordia.   × 53.

Figs. 26, 27. Longitudinal sections of old flower-heads, showing large-celled axial tissue and no definite organ at the apex of the head ; compare the densely staining bracts, sepals, and carpels in 27 with those in 26.   × 26.

Fig. 28. Series of longitudinal sections of a carpel (legume) showing the midrib proceeding strongly into the style in contra-distinction to the bundles that supply the ovules. The midrib passes up the curved side (right hand) of the carpel, the style appearing to spring from above the appressed margins of the carpel (left hand (*cf.* figs. 26, 27, 36–41). Note placental hairs.   × 63 approx.

<div align="center">PLATE 24.</div>

Figs. 29–31, of anthers.   29, of a model cut open to show disposition of pollinia (*not* dehiscence).   30, anther cleared in cedar-wood oil, showing eight pollinia and residual ' exine ' of tapetum (*t.*), × 173 approx.   31, transverse section of anther showing dehiscence, endothecial thickenings, and residual ' exine ' of tapetum (*t.*), × 125 approx.

Fig. 32. Model of a pollinium with one tetrad dissected.

Fig. 33. Transverse section of flower-head above the apex of the axis, showing three legumes with midrib (B), two marginal bundles (*b.*), and appressed epidermes (*e.*). The midrib side of the legume is away from the flower-head axis.   × 100.

Fig. 34. Four transverse sections at different levels of the style, ovary, and base of a sterile legume, showing the ' coiled leaf ' structure, presence of midrib primordium (B), but no primordia of marginal bundles. Sections of the filaments surrounding the style are included in the upper one of the series.   × 150.

Fig. 35. Oblique longitudinal section of flower (unopened) showing a small flower growing, as a continuation of the floral axis, past the legume of the large flower.   × 120 approx.

Figs. 36, 37. Transverse sections of the legume respectively below and above the upper limit of the placenta, showing that the midrib (B), proceeds into the style, but not the marginal bundles (*b.*). The appressed marginal epidermes can be made out at *e.*   36, × 200 ; 37, × 150.

Figs. 38, 39. Longitudinal sections of legume, marginal (adaxial), and midrib (abaxial) sides respectively.   38 passes outside the marginal bundles and 39 inside the midrib (*e.*), line of epidermes.   × 200.

Figs. 40, 41. Transverse section of legume, showing clearly the appressed marginal epidermes (*e.*), the midrib (B), and the marginal bundles (*b.*).   41 is a faint print of 40, outlined to show up the features of 40.   × 150.

Fig. 42. Section of flower with sterility in the androecium, due to collapse of the sporogenous tissue (S). An abnormal meiosis, with lagging of chromosomes is shown at 1, × 200.   Fig. 42 *a*. Meiotic spindle (*l*, fig. 42) with lagging of chromosomes, × 1,800.

Figs. 43, 44. Consecutive longitudinal sections of an ovule, above the funiculus, showing two mother-cells, with a well-distributed pachytene in one and the synizetic condition in the other. Notice the line of separation between the parietal tissues (S). × 750.

Fig. 45. L. S. of mature ovule, showing vestigial inner and outer integuments, *ii.* and *oi.* Notice the persistence of the parietal and lateral receptacle tissues. The placental hairs are also to be seen under the ovule. × 480.

Fig. 46. Section of two anther lobes showing the relative size of the mother-cells before (left) and at (right) synizesis. × 500.

Fig. 47. Two microspore mother-cells, the upper of which shows a ' brochonema ' formation. There are about thirteen loops, not all in the plane of focus. × 680.

Fig. 48. Tapetum and a typical heterotypic metaphase spindle in the anther. Note the large tapetal nuclei. × 750.

Fig. 49. Pollinium-mother with the interkinetic nuclei in one plane. Note the cytoplasmic fibres perpendicular to the inner walls, also the peripheral chromosomes. × 750.

PLATE **25.**

Fig. 50. Approximately transverse sections of two adjacent pollinium-mothers, showing the chromosomes on the pachytene thread. Note the prominent inner tapetum. × 1,560.

Fig. 51. Longitudinal section of anther-lobe, showing pachytene-stage in one sporangium and heterotypic metaphase in the other. Note the great depth of the outer parietal layer (*p.*) at the right, and its narrowness at the left (corresponding to the groove) of the anther. × 710.

Figs. 52 54 *a*. Show the polar view of heterotypic anaphase groups in a pollinium-mother. 53 and 54, corresponding to the silhouette drawings 53 *a* and 54 *a*, are on the one spindle, section of whose fibres can be seen at the bottom of 52. A group from another spindle is shown in 52 and 52 *a* (silhouette). 53 includes one lobe of the anther and shows the deep outer parietal layer (*p.*). There are thirteen chromosomes, similarly arranged in each group. 52, 53, 54. × 1,065.

Fig. 55. Surface-view and sections of pollinia, also showing the endothecium in longitudinal view (F) and the ' exine ' of the tapetum (*t.*). × 240.

Fig. 56. Edge view of a pollinium showing the completely formed micropores (uninucleate), the prominent tapetum (*t.*), and the deep cells of the remaining outer parietal layer (*p.*). × 600.

Fig. 57. Oblique longitudinal section of anther showing a plate of four mother-cells at synizesis, the tapetum (with nuclei drawn), and two parietal layers. × 509.

Fig. 58. Longitudinal section of young ovule, showing the mother-cell at synizesis, and the first division of the primary parietal cell. × 509.

Fig. 59. Four consecutive sections (*a–d*), as indicated in *e*, of a pollinium-mother at diakinesis. There are shown thirteen pairs of chromosomes in the nuclei, except that those in the left-hand nucleus are rather confused. Types of configuration and the presence of trabants are indicated. Note the four double bodies at the edge of the cytoplasm of the cells. × 1,330.

Fig. 60. Two consecutive sections of two microspore mother-cells at early heterotypic metaphase, showing thirteen pairs of chromosomes and three poles of each spindle. × 966.

Fig. 61. Two anaphase groups of one spindle of homotypic division in microsporogenesis, each showing thirteen chromosomes, with trabants on some. × 1,310.

Fig. 62. Longitudinal section of a megaspore mother-cell at late diakinesis. The chromosomes in the centre are too mixed to determine the number accurately, but thirteen is indicated. × 1,033.

Some phylogenetic considerations on the genus *Oenothera*, with descriptions of two new species. By Professor R. RUGGLES GATES, F.R.S., F.L.S.

(PLATE 26)

[Read 4 February 1932]

THE systematic history of the genus *Oenothera* has been exceptional in several respects. After being neglected by the professional systematists of the nineteenth century it was given a unique place in the history of biology through the experimental work of de Vries on the mutations of *Oenothera Lamarckiana*, which was one of a number of species naturalized in various parts of Europe during the last three centuries. This work naturally directed attention to the home of the genus in North America, where an attempt was made to determine the original location of *O. Lamarckiana* Ser., *O. biennis* L., *O. grandiflora* Soland., and other species. This resulted in successfully tracking *O. grandiflora* to its original home in Alabama (MacDougal, 1905), where Bartram first discovered it about 1773. *O. syrticola* Bartl., which is the *O. muricata* of most European authors, is recognized from the Holland sand-dunes and also from Wood's Hole, Mass., and Orange, Conn. *O. parviflora* L. has been identified (MacDougal, Vail, and Shull, 1907) as native to South Harpswell, Me., and the same form was grown in the Botanic Garden, Madrid, in 1906, presumably from an early introduction. There is evidence that it formerly occurred as far south as Maryland and Virginia and that it is still common near Washington. The typical form of *O. biennis* L. is known only from the Holland sand-dunes, and has never yet been found in America (Bartlett, 1913). These are the only species which were described by European botanists and which are known to be now native of America. *O. simsiana* Ser., which is closely related to *O. Hookeri* T. & G., probably still exists in Mexico.

The decade 1905–15, following de Vries's classical work ' Die Mutationstheorie ', was a period in which considerable interest was shown by a few geneticists, and incidentally several new species, especially from the Western States, were described by systematists. The attempt to identify in America various species long known in Europe gradually led to recognition of the fact that many more native species existed than had been supposed. Bartlett (1914) was for some years active in delimiting new species in his cultures from seeds collected in many parts, but especially in Maryland, Virginia, Kentucky, Minnesota, and California, and he has contributed most to the purely systematic study of the genus in America.

In my monograph on *Oenothera* research (Gates, 1915), Chapter II was devoted to a synopsis of the general characters, together with a map and brief characterizations of the species, with notes on the twenty-nine species and eight varieties

then recognized. To this was added a list of eleven more species, mostly described
or recognized about the time that book appeared.   Chapter III of that mono-
graph dealt with the cultural history, including the early accounts of *Oenothera*
in Europe as recorded in botanical works of the seventeenth and eighteenth
centuries, as well as records of many early specimens in various European
herbaria.   A study was made of the numerous specimens in early herbaria
or drawings of evening primroses, frequently with polynominal names, in the
works of Alpino, Columna, Parkinson, Morison, Barrelier, Miller, and others.
Tentative attempts were made to identify some of these as belonging to or
nearly related to modern recognized species.   Owing to the recognition of many
other species of *Oenothera* since then—species with large or small flowers,
broad or narrow leaves, etc.,—these identifications cannot be regarded as more
than approximate indications of relationship, as the early drawings were not
sufficiently accurate to distinguish between various species having similar
habit, flower-size, or leaf-width.

We now know that another important consideration enters into all attempts
to identify specimens or naturalized plants existent in Europe by comparing
them with American forms.   This is the fact that all the *Oenothera* species of the
subgenus *Onagra* cross rather freely, producing new forms different from either
parent, forms which will then breed more or less completely true, this depending
generally on the amount of chromosome linkage (catenation *) present in the
hybrids during meiosis.   Such crossing has clearly taken place among naturalized
forms in various European localities.   Many of the wild North American species,
especially the small-flowered ones, are now known to show complete catenation
instead of free assortment during the period of meiosis.   Yet, being heterozy-
gous, made up of two complexes (a term introduced by Renner), they produce
two different hybrid types even when crossed with a homozygous form.   By this
means a number of species have been shown to be composed of two complexes,
in some species much alike but in others surprisingly different.   For instance,
among unpublished results the size of flower belonging to one complex may be
nearly twice that belonging to the other complex of the same species, or the
foliage characters of the two complexes may be extremely unlike each other
and different from the phenotype or external characters of the species.

Without going further into the genetics of these crosses we may say that many
species of *Oenothera* when crossed together will give two new ' species ', different
from either parent, and yet, although heterozygous or made up of two complexes,
breeding true because of the catenation of their chromosomes during meiosis.
De Vries (1907) originally described this condition in *O. biennis* × *Lamarckiana*,
long before anything was known of the different chromosome linkages.   From
this cross two types are produced, which he called twin-hybrids, naming them
laeta and *velutina*.   Both breed true in general, and they differ from each
other in foliage as markedly as two ordinary Linnean species.   They are

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* This term was introduced (Gates, 1931) to distinguish between physical linkage of
chromosomes and genetical linkage of genes,

almost as unlike in foliage characters as are the two parents. This twin-hybrid behaviour was amply confirmed (Gates, 1913) a few years later.

From these and many other crosses Renner (1917 *a*) recognized the principle of complexes, naming the complexes in *O. Lamarckiana*, for example, *gaudens* and *velans*. By the extension of this method many wild species have been analyzed into their two complexes, and this kind of analysis has become an important field of research. In *O. Lamarckiana* the *velans* and *gaudens* types of pollen grain are both functional and are distinguishable by their size and the shape of their contained starch-grains. Both types of megaspore are also functional, but the gamete combinations *velans . velans* and *gaudens . gaudens* fail to develop, and hence half the seeds of *Lamarckiana* are empty. In various other species one of the pollen or egg types may be non-functional, so that all the functional pollen may contain one complex and all the functional eggs the other. Thus in *O. biennis*, in which Renner (1917 *b*) named the complexes *albicans* and *rubens*, all the functional pollen is *rubens*, while the developing embryo-sacs are of both types. In *O. strigosa* and other species one complex is viable in the pollen and the other in the eggs. This condition, in which the two sexes of a plant differ in their genetic qualities, was called heterogamy by de Vries (1911). Such species will breed true but will give different reciprocal hybrids when crossed with another species. Various species taken directly from the wild in North America show similar conditions, and there is reason to believe that their chromosome linkage is the fundamental cause of their behaviour as permanent crypthybrids, i.e. as forms which breed true although heterozygous. It cannot be supposed that conditions in the genus *Oenothera* are unique, and catenation in a less degree is already known in *Datura*, *Pisum*, *Rhoeo*, *Campanula*, *Aucuba*, and other genera. The condition is one, therefore, of which the systematist needs to take cognizance.

In general it may be said that the species-hybrids of *Oenothera* are intermediate between their parents but usually nearer one parent than the other, and the degree of resemblance may vary from character to character. Most frequently they are rather strongly patroclinous, but in some cases they are matroclinous. It also occurs that a hybrid may resemble one parent species more strongly in one stage of its development and the other parent at a later stage. This is a phenomenon to which geneticists have as yet given very little attention, but it is worthy of much further study. This change of appearance frequently leads to the recognition of two apparent types in a hybrid culture when there is in reality but one type, the difference being due to some plants having passed out of the rosette stage earlier than others. It is sometimes a matter of much difficulty to determine whether the differences represent developmental stages or distinct types, but this can usually be settled by careful observation of all stages in development. In a similar way the complexes of a species, when combined, produce the phenotype of that species ; one of its complexes is frequently much more like the phenotype than the other, while in various characters the complexes may both be different from the phenotype.

It may also be pointed out here that whereas some of the twin combinations (e.g. *laeta* and *velutina*) differ as much in foliage in the rosette as in the flowering stage, wild species which are very similar as rosettes frequently diverge widely in the flowering stage. In such cases the rosette may represent a more conservative ancestral stage from which divergence in other characters has taken place. *O. argillicola*, *O. levigata*, and *O. scitula*, described from one locality in West Virginia, are an example, *O. grandiflora* and *O. Tracyi* from Alabama another.

In the light of the above-mentioned facts it is clear that some of the species of *Oenothera* described from European localities and showing chromosome catenation may have arisen in Europe from natural crosses occurring between forms brought accidentally or otherwise from America. If they have arisen as crosses between species which are widely separated in America then they would not be found in America at all. In such cases it would be futile to search for the species on Canadian or American soil. Close examination of various European populations of *Oenothera* indicates that some of them are, or contain, hybrid swarms, giving rise to new and relatively constant species. Thus *O. germanica* Boedijn from Rahnsdorf, near Berlin, and *O. Bauri* Boedijn from Friedrichshagen bei Berlin apparently represent such species. A cultural study (Gates, 1915 *a*) was made of such a swarm from the Lancashire coast. Some of the forms isolated in culture probably fail to develop beyond the seedling stage in natural conditions of competition. It is possible, but improbable, that *O. ammophila* Focke may be such a species, although there is at present no clear indication which species would constitute its parents. It resembles one of the new species described below from Nova Scotia, but there is no evidence at present to indicate that this new species is historically or genetically related to *O. ammophila*. In this connection it may be recalled that Davis (1916, 1924) produced a form resembling *O. Lamarckiana* in some respects by crosses between *O. franciscana* Bartl. from California and *O. biennis* Linn. from Holland. But this ' *neo-Lamarckiana* ' also showed marked differences from *Lamarckiana* in certain features, such as the presence of red papillae on the sepals, and, despite much controversy on the subject, there is no adequate reason for supposing that *Lamarckiana* arose from this cross. The catenation in *neo-Lamarckiana*, which might serve as a further test, is at present unknown.

Since, as already stated, the Oenotheras in America, especially the more northerly and small-flowered forms, from all lines of evidence appear to constitute a swarm of permanent crypthybrids, it might be asked whether they should be described as species. If the criteria of species are that they should breed reasonably true and differ in numerous characters displayed throughout their development, then it is impossible to deny specific rank to these forms, and in any case it is necessary to give them names in order to deal with them. It is possible that, after much wider study, relationships may be disclosed between them, or evidence regarding their precise origin which will make it possible to reduce many of them to lower rank, but any such attempt at the present time would necessarily be based upon resemblances which would probably prove to be superficial in character and not of phylogenetic significance. Hence, although

a host of these wild forms must be described as new species, nevertheless it must at the same time be recognized that by judicious interspecific crosses it is possible to create as F_1 hybrids an indefinite number of forms which would have perhaps equal claim to rank as species so far as the distinctness of their characters is concerned, although some of the hybrid types might not stand the test of survival under natural conditions of competition with other vegetation, and some would be non-viable or lethal combinations. It is probably too much to hope that wild American species can be exactly constituted by crosses made between any of the existing American forms.

It has been generally accepted by students of the genus that its home was in Central America, from whence it has spread northwards since the Pleistocene. The South American forms have large flowers and, so far as known, belong mostly to the subgenus *Raimannia*. In North America the subgenus *Onagra* was probably derived from *Raimannia*, and so began with large flowers. The subgenus *Raimannia*, which includes such species as *O. humifusa* Nutt., *O. sinuata* L., *O. heterophylla* Spach, *O. catherinense* Camb., and *O. Agari* Gates, differs from *Onagra* in having small and narrow leaves, sepal tips subterminal and sprung, red at tip; capsules slender, linear, seeds somewhat rounded. The South American forms belong mainly to *Raimannia*, the North American mainly to *Onagra*. Some South American species are transitional, so that a separate genus cannot be recognized. *O. campylocalyx* Koch & Bouché is the only true *Onagra* I have seen from South America. ' It has long hypanthia, sepal tips terminal, and petals turning red in drying, like some species from western North America. In *O. angustissima* Gates the sub-terminal sepal tips, very narrow leaves, and slender side branches suggest *Raimannia*.

It was pointed out long ago (Gates, 1915) that there is a general and progressive decrease of flower-size in *Onagra* in passing northwards to higher latitudes; it therefore seems clear that as the Oenotheras moved northwards after the ice age they gave rise, through a series of mutations, to forms with smaller and smaller flowers. This is partly confirmed by the studies already made on inheritance of length of petal (Gates, 1917, 1923, 1931, 1932). The flowers range from about 60 mm. (length of petal) in *O. macrosiphon* Wooten & Standley, from New Mexico, to about 5 mm. in *O. parviflora* L., which apparently ranged from Maine to Virginia, being constant for each species within quite narrow limits. It will thus be seen that the relation between latitude and flower-size is by no means a close one, but it represents a general tendency, the species with smallest flowers occurring mainly in Canada and the Northern States, while those with large flowers occur mainly in Mexico and the Southern States. Boedijn (1924) agrees essentially with the above view and regards the whole subgenus *Onagra* as derived from ' *Euoenothera* ', which has large flowers and appears to be native to South America.

Decrease in flower-size has been accompanied by lesser pollen production. As the small flowers are mostly self-pollinated, while the larger flowers usually have a longer style and are scarcely pollinated without the visits of insects, less pollen will usually be required for the small flowers to produce seeds. In this

sense the small flower is a more efficient reproductive mechanism and will usually produce a greater abundance of seeds than the large-flowered, open-pollinated species. This marked difference in seed production is easily observed when species are grown side by side in an experimental garden. This helps to account for the wider dispersal of the small-flowered species, and since the chromosome catenation in these species results in their remaining permanent heterozygotes composed by the union of two different complexes, the disadvantages which might otherwise result from inbreeding do not arise in them. The hybrid vigour arising from their heterozygous condition may indeed furnish the reason why the permanent crypthybrids persist in nature while the more nearly homozygous derivatives with less catenation, which would be expected to occur from time to time, fail to survive under natural conditions of competition.

Broekens (1925), who discusses the phylogeny of the whole family of Onagraceae, reaches conclusions similar to those above, placing the large-flowered species at the base of the genus. In this connection it is interesting to note that *O. Lamarckiana* has produced two rare small-flowered mutations, *O. de Vriesii* and *O. bienniformis*. Whether the small flower is recessive in crosses with *O. Lamarckiana* and other large-flowered forms is unknown, but it is significant that in species-crosses (see Gates, 1931) the small flower is usually more or less completely dominant to the large (see Gates, 1932). This would mean that a series of dominant mutations had occurred as the genus moved northwards. It may also be pointed out here that *O. Tracyi* Bartlett (1911) is essentially a small-flowered segregate from *O. grandiflora* Soland., the two growing together in the same locality, having similarities in foliage and buds, and no doubt intercrossing. It would be interesting to know whether the small flower is dominant in this hybrid.

Johansen (1929) proposes a phylogeny of the Onagraceae based primarily upon chromosome number, but as he begins with the highly improbable suggestion that the family arose from a cross between an aquatic form having four chromosomes (haploid) and a terrestrial form with seven we need not follow his speculations further.

Another striking fact, which fits in with our conception of the evolution of the genus, is that the only wild species of *Oenothera* in America known to be relatively homozygous and free from chromosome catenation is the large-flowered *O. Hookeri* T. & G., while its segregate *O. franciscana* Bartl. has five pairs and a ring of four. The quite small-flowered species hitherto examined from Canada and the Northern States all have a complete ring of fourteen chromosomes. This includes *O. angustissima* Gates, *O. nutans* Atk. & Bartl., and *O. pycnocarpa* Atk. & Bartl. (all from Ithaca, N.Y.), *O. eriensis* Gates, from Lake Erie, *O. novae-scotiae* Gates from the Annapolis Valley, and *O. syrticola* Bartl. (=*muricata* auctt.) from Holland, Massachusetts and Connecticut. Unfortunately, the catenation in other small-flowered species is still unknown. *O. ammophila* Focke, from the European sand-dunes, has a ring of twelve with one free pair. It was formerly believed (Davis, 1909) that *O. grandiflora* Soland. was a homozygous species with seven free pairs of chromosomes, but

Gerhard (1929) has since found that the true *O. grandiflora* has a ring of twelve and one free pair (like *O. Lamarckiana*), its derivative mutation *ochracea* having seven free pairs, while Cleland (1931) has recently found a ring of fourteen in his strain.

From the various considerations mentioned above the indications seem clear that the subgenus *Onagra* began in the south as large-flowered, homozygous species without catenation, and that in passing northwards they developed progressively increasing chromosome linkages as a result of crosses between distantly related species. That such catenation can arise as a result of crosses between two homozygous Oenotheras without any catenation has recently been shown experimentally (Gates & Catcheside, 1931). It clearly would be unsound, however, to draw the contrary conclusion that a homozygous form (without catenation) cannot be derived from ancestors which show catenation. Indeed, this change to a more homozygous condition with seven free chromosome pairs has been known to occur in a number of mutations from different species under experimental conditions. Thus *deserens* and *blandina* are different secondary mutations from *O. Lamarckiana*, and *ochracea* is similarly derived from *O. grandiflora*. Among wild European forms *O. purpurata* Klebahn is homozygous and has seven free pairs of chromosomes. It was described with other forms from the Lunenburger Heide of Northern Germany (Klebahn, 1925) and is almost certainly a homozygous derivative from introduced heterogamous forms showing catenation.

Thus we arrive at the conception of a swarm of crypthybrid native species occupying a large part of Canada and the United States. This swarm remains to be examined from the points of view of the systematist, the geneticist, and the cytologist. Most of the species hitherto known occupy only local areas, and there are huge gaps in the map between. Many of these will doubtless be occupied by other local species, and sometimes an area will be occupied by several species. What happens where the distributional areas of two species overlap is unknown, but crossing and the production of twin types, with further crosses leading to the production of a swarm of intermediate and mutational types, may be expected. Only by combined investigation of the catenation (cytology), the complexes through series of crosses (genetics), and the phenotypes (systematics), including their pollen and seed sterility and their megaspore behaviour, can an analysis of the complicated history of the genus be pushed further.

It has been suggested in the case of *Crataegus* (see Marie-Victorin, 1929) that the clearing of the forests after the advent of civilized man in America may have enabled the species to cross and so produced a hybrid swarm within the last three centuries. Whether something of a similar kind might have been a factor in the production of the diversity of forms in *Oenothera* is too early to say. There is the important difference that *Oenothera* is a herb, not a tree, and that its natural dispersal in America is much wider than that of *Crataegus*. It seems clear that in Europe various forms of *Oenothera* have arisen partly through crossing during the last three centuries, and it appears probable that man's disturbance of the natural vegetation in various parts of America

will also have led to recent collisions between species, with similar results. On the other hand, it is likely that *Oenothera* species in America had already occupied all parts of the continent as locally differentiated species before the advent of civilized man.* In any case there is, as indicated above, abundant evidence of an earlier and more important evolution in the genus, beginning with large-flowered forms in the south and ending with the smallest-flowered species in the most northerly latitudes in Canada which the genus has yet reached. During this earlier period great movements were taking place which would lead to ample intermingling of species as they pushed northwards into relatively unoccupied territory. The evidence strongly suggests that during this period dominant mutations for smaller flowers have occurred independently many times in different populations and lines of descent in different parts of the vast American continent. It is equally clear that the *cruciata* mutation for narrow petals has occurred independently in various lines of descent, but so far as known this mutation has been confined mainly to the Eastern part of the continent.

The intention of this paper is by this brief introductory account of the present position in the genus *Oenothera* to stimulate a more thorough study of the systematics and distribution of the genus as a whole. To this end the author will be glad to receive seeds from any wild *Oenothera* anywhere, together with an exact indication of the locality where they were collected. Only in this way will it be possible to determine the lines along which the evolution of the genus proceeded and the relative parts played by hybridization, mutation, and segmental interchange of chromosomes. In this genus satisfactory herbarium specimens are difficult to make, and used alone are quite inadequate for discriminating some of the numerous species. It is only from cultures that their characters can be properly compared and understood. Many workers are necessary, and it is hoped that American botanists will show a renewed interest in the genus.

The two new species are as follows :—

OENOTHERA AMMOPHILOIDES Gates & Catcheside, sp. n..

Rosette leaves, spathulate, 20×5 cm., long-tapered towards the base, apex mucronate-acuminate, margin wavy when young, becoming flat, distantly repand-denticulate, especially basally, deep glaucous green, thick and somewhat leathery, midrib white on both upper and lower surfaces (Pl. 26. figs. 1, 2).

Stem strongly bent at tip (10–12 cm.), the bracts of this portion being horizontally oriented (see Pl. 26. fig. 3), giving a characteristic appearance. The buds, and later the capsules, tend to adopt a vertical position. Stem 0·6 metres long, terete, wavy, green, with very numerous red papillae and long patent hairs, stem becoming red on portions exposed to light.

* They are frequently weeds in cultivated soils, and may thus have been spread in crop-seeds in certain cases.

Stem leaves like rosette leaves but smaller and linear-elliptic, tapering gradually at base. Bracts smaller, oblong-lanceolate, midribs pink below and bearing numerous red papillae. Bud cone stout, somewhat quadrangular, 13×5.5 mm., hypanthium yellow, 25×3 mm. expanding to 6 mm. at the top, sepals yellow-green, becoming red where exposed to light, close-set with red papillae and subpatent soft hairs, sepal tips 5 mm. long, not appressed, green, covered with short nearly appressed hairs. Petals 18×23 mm., obcordate with narrow sinus bearing a short apiculate point, yellow, contiguous. Style short, stigma surrounded by the anthers, style projecting 6 mm. from hypanthium tube. Stigma lobes not opening out flat, 11 mm. long, fairly slender. Filaments 8–9 mm. long, anthers 10 mm. long, ovary cylindrical, 18×3.5–4 mm. Inflorescence rather dense, elongating in fruit. Fruits strongly quadrangular, 50–60×8–10 mm., green, tinged with red,[*] bearing long hairs which arise from red papillae (Pl. **26**. fig. 4).

Resembles *O. ammophila* closely in rosette stage, and in habit (especially the bent stem) until flowering begins, differing however in the wavy margin of the younger rosette leaves. The stems, sepals, and fruits differ in the presence of abundant papillate hairs, the flowers are much larger and the fruit capsules are extraordinarily long compared with all other Oenotheras hitherto described except *O. Reynoldsii* mut. *bilonga* (La Rue & Bartlett, 1918).

Although *O. ammophiloides* has very long and stout capsules, yet the ovaries at flowering are not of exceptional length. A capsule was found to contain 306 seeds and 201 undeveloped ovules. A capsule of *O. pycnocarpa* by comparison contained 407 seeds and 106 undeveloped ovules, although the capsule was only 35 mm. in length and 9 mm. broad. In the mut. *bilonga* of La Rue & Bartlett there was a great increase in the number of ovules, i.e. about 1150 per capsule in comparison with 800 in the typical form. The seeds of *O. ammophiloides* are not visibly larger than in other species, but they are more loosely packed in the long capsules.

Diagnosis : Biennis. Folia radicalia spatulata, longe petiolata, circa 20 cm. longa et 50 mm. lata, subglauca, pleni viridis coloris, costa alba. Caulis obliquus, foliis horizontaliter orientatis, teres, viridis, multis longis pilis rubro-tuberculatis instructus, rubescens ubi lucem accipit. Folia caulina minora quam radicalia, lineari-elliptica. Alabastrae aliquantum quadrangulares ; sepala rubescentia ubi lucem accipiunt, densē multis longis pilis rubro-tuberculata. Petala flava, circa 18 mm. longa et 23 mm. lata, obcordata cum angusto sinu ferente apiculam brevem. Antherae stigmata attingentes. Capsulae quadrangulares, ad 60 mm. longae, erectae, virides, rubro-tinctae, longis pilis rubro-tuberculatis instructae.

Grown in Regent's Park Gardens from seeds collected by Jacques Rousseau, 21st August, 1930, at Guysborough, Nova Scotia, and transmitted by Professor Marie-Victorin.

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[*] In the strong light of Ithaca, N.Y. (in the genetic garden, 1932), the fruits develop numerous small dark red blotches.

OENOTHERA VICTORINI Gates & Catcheside, sp. n.

Rosette leaves broad, smooth, elliptical, 24×6·5 cm., midribs narrow, pink above, paler below (Pl. **26.** figs. 5 & 6). Leaves medium green in colour, rosette and basal stem leaves turning a bright red in fading. These leaves have pointed basal teeth. Stem leaves elliptical, bracts very small, narrow and wavy. Stem erect, green, terete, long basal ascending branches, short branches at base of inflorescence, with sparse hairs arising from green papillae. Inflorescence very dense, scarcely elongating. Buds cylindrical, pointed, yellow-green, bud cone 20×6 mm. (Pl. **26.** fig. 7). Sepal tips short (4 mm.), spreading, green, red-tipped, sparse hairs from green papillae on sepals ; hypanthium yellowish, 35×2·5 mm., expanding to 7 mm. wide at top. Petals 26×30 mm., obovate, sinus scarcely developed, bright yellow, overlapping slightly, style short, stigmas surrounded by anthers, style projecting 11 mm. from hypanthium, stigma lobes spreading almost flat, 9 mm. long, fairly slender. Filaments 12 mm., anthers 10 mm., ovary cylindrical, green, 17×3 mm. Fruits green, somewhat quadrangular, long and slender, much tapered, reaching 45×7 mm., with a few appressed hairs arising from green papillae (Pl. **26.** fig. 8).

The species resembles *O. pycnocarpa*, *O. nutans*, and *O. novae-scotiae* in general habit, but differs conspicuously from the former in the colour change of the leaves on fading. *O. novae-scotiae* also changes colour but to a darker rusty red. The flowers are much larger than in these species. The leaves are without the characteristic basal jagged teeth of *pycnocarpa*, which are still more strikingly developed in *O. novae-scotiae*. In the absence of red papillae it agrees with *pycnocarpa* and *nutans* and differs conspicuously from *novae-scotiae*. *O. nutans* is conspicuously different in leaf shape.

Diagnosis : Biennis. Folia radicalia lata, lēvia, elliptica, 24 cm. longa et 65 mm. lata, costa angusta, superne rubicunda, infra pallidiora. Folia medii viridis quae languescentia rubescunt, cum dentibus acutis ad basim. Folia caulina elliptica, bractae parvulae, angustae, fluctuosae. Caulis erectus, viridis, teres, sparsē pilis virido-tuberculatis instructus. Spica densissima, vix se extendens. Alabastrae cylindricae, acutae, flavo-virides, sepala sparsē pilis viridi-tuberculatis instructa, apices sepalorum expansi, virides, rubri ad extremum. Petala flava, paulum superjacentia, obovata, sinu vix formato, antheres stigmata attingentes. Capsulae virides, aliquantulum quadrangulares, longae et graciles (ad 45 mm. longae) quae ad summam minores fiunt, pilis appressis virido-tuberculatis instructae.

Grown in Regent's Park Gardens from seeds collected by Professor Marie-Victorin, September 1930, at St. Hubert, Quebec, near Montreal.

The following table is a brief synopsis of the known species of *Oenothera* belonging to the natural North American subgenus *Onagra*. The main forms described in the naturalized populations found in various parts of Europe are also included. In each case the distribution or the locality from which it was described is given, together with the flower-size, as these bear directly upon the relationships of the species. It would be unprofitable to attempt

a more detailed comparison of phenotypes in the present state of our knowledge, but various known differences between related forms are pointed out. Species evidently nearly related are linked by brackets. A useful synopsis of species, giving full references to the literature, is to be found in Lehmann (1922).

TABLE I.

Species.	Type-locality or range.	Petal-length. mm.
O. grandiflora Soland.	Dixie Landing, Alabama.	35–40
O. Tracyi Bartl.	„ „ „	20–25
O. erythrosepala Borbás	Near Budapesth, Hungary.	50
O. suaveolens Desf.	Forest of Fontainebleau (Blaringhem). Naturalized elsewhere in western France.*	—
O. Lamarckiana Ser.	Hilversum (Holland), Lancashire coast, Sweden, etc. †	ca. 40
O. multiflora Gates	Near Birkenhead, Lancashire.	43
O. rubrinervoides Gates	„ „ „	ca. 40
O. tardiflora Gates	„ „ „	small.
O. rubritincta Gates	„ „ „	32
O. Hookeri Torr. & Gray var. angustifolia Gates ‡	Montana to California and Mexico. Asphalt, Utah.	40–45 35
O. guttata Greene §, n. n........	Kingston, New Mexico (Herb. Brit. Mus.). (See Gates, 1915, p. 30.)	30–40
O. Hookeri var. semiglabra Gates, 1915 ‖.	Calif. specimen, J. G. Lemmon, 1875, in Herb. Brit. Mus.	ca. 45
var. parviflora Gates, 1915 ..	Kamloops, B.C. Specimen, John Macoun, 1889, Herb. Brit. Mus.	12–14
O. purpurata Klebahn	Bevensen, North Germany (Klebahn, 1925).	22
O. Hewettii Ckll.	Rito de los Frijoles, New Mexico.	ca. 38
O. franciscana Bartl.	Carmel Beach, Monterey Co., Calif.	ca. 36
O. venusta Bartl.	San Bernardino, Calif., and southwards.	42
var. grisea Bartl.	Riverside, California.	42
O. Jepsonii Greene	Sacramento River, California.	10
O. hirsutissima Rydb.	New Mexico and Colorado.	40
O. Simsiana Ser.............	Mexico Valley.	40
O. Jamesii Torr. & Gray	Oklahoma, Texas, Arizona, Utah.	40
O. Clutei A. Nels.	Utah, Arizona.	—
O. macrosceles Gray	Northern Mexico.	ca. 35
O. longissima Rydb.	Utah and Arizona.	40
O. irrigua Woot. & Standl. ...	New Mexico.	35
O. macrosiphon Woot. & Standl.	Organ Mountains, New Mexico.	50–60

* A specimen, apparently of O. suaveolens, was collected wild in America by Michaux.

† Boulenger (1907) described a population consisting of O. Lamarckiana with O. biennis and their hybrids at La Grande St. Cast, near St. Malo, Brittany.

‡ Based on a specimen in Herb. Brit. Mus. collected by Marcus E. Jones (Gates, 1915, p. 30). Differs in having narrower leaves (8–12 mm.), slender, bright red stems, leaves very obscurely denticulate.

§ Leaves 8–12 mm. wide, pointed, conspicuously repand-denticulate, taller than var. angustifolia.

‖ Absence of white pubescence, buds nearly glabrous.

Species.	Type-locality or range.	Petal-length. mm.
O. Macbrideae (Nelson) Heller..	Twilight Gulch, Owyhee Mountains, Idaho.	44–30
O. ornata (Nelson) Rydb.	Foothills and mountain slopes near Boise, Idaho.	ca. 25
O. argillicola Mackenzie	Southern New York, Maryland, Virginia, and W. Virginia.	40–45
O. levigata Bartl.............	White Sulphur Springs, W. Virginia.	17
O. scitula Bartl.	,, ,, ,, ,,	12
O. biennis L................	Type known only from Holland coast. English coast at Formby, Lancashire.	20
var. leptomeres Bartl.	Sandpoort and elsewhere in Holland ; Lüneberg, Germany.	—
O. rubricaulis Klebahn (1914)..	Bevensen, Lunenburger Heide.	19–21
O. chicagoensis Renner........	O. biennis, Chicago, de Vries (1913). Seeds from near Chicago and from the Missouri River, Mo.	—
O. Reynoldsii Bartl.	Knoxville, Tennessee, common.	24–28
O. Oakesiana (Robbins) S. Watson.	St. John River, N.B. and Quebec to Mass., New York and west to S. Dakota, Minn., and Colorado.*	13–15
O. rhombipetala Nutt.	Red River, Arkansas, Minneapolis. (De Vries, 1913, p. 52.)	15–20
O. Tidestromii Bartl.	St. Mary's Co., Maryland.	20
O. stenopetala Bicknell	Nantucket Island.	10–22
O. pratincola Bartl.	Lexington, Kentucky, common.	18
O. numismatica Bartl.	,, ,, rare.	18·5
O. furca Boedijn	North Town Junction, Minnesota. Coll. de Vries (1913) in 1904.	ca. 18
O. disjuncta Boedijn..........	North Town Junction, Minnesota. Coll. de Vries (1913) in 1904.	ca. 13
O. Alsbergi Bartl. †	North Town Junction, near Minneapolis. (See de Vries, 1916, p. 244.)	—
O. strigosa (Ryd.) Mack. & Bush.	Minnesota, Utah, and Washington State to Kansas and New Mexico.	15–20 ‡
O. Cockerelli Bartl.	Boulder, Colorado.	—
O. procera Wooton & Standl. ...	New Mexico.	12–14
O. canovirens Steele	Illinois.	10–14
O. subulifera Rydb.	Montana, Forks of the Madison.	—
O. depressa Greene	Custer, Montana.	ca. 10
O. cheradophila Bartl.	Wyoming and Washington State.	8
O. angustissima Gates	Ithaca, New York.	15–20
O. pycnocarpa Atk. & Bartl. ..	Ithaca, New York, and Flint, Mich.	13–18
O. nutans Atk. & Bartl.	Ithaca, New York, and Harve de Grace, Md.	15–22
O. ruderalis Bartl............	Chevy Chase, Md., and near Washington and Baltimore.	17

* Probably this species in the strict sense is confined to the Atlantic coastal region, from the St. John River to New York. The western form differs in certain particulars and has larger flowers (petals 20 mm.).

† Low, with thick dark foliage and very small flowers. See figure in de Vries (1913), p. 35, fig. 10, left.

‡ In some races the petal-length is only 5 mm.

Species.	Type-locality or range.	Petal-length. mm.
O. gauroides Hornem.........	Common in Md. and Va.	—
O. brevicapsula Bartl.........	Chevy Chase, Maryland.	20
O. stenomeres Bart.	Chevy Chase and Bethesda, Montgomery Co., Maryland.	10–11
O. rubescens Bartl.	Nantucket Island, Mass.	16
O. cymatilis Bartl.	Sawyer, Berrien Co., Mich.	16
O. insignis Bartl.	Lake Superior, near Duluth, Minn.	16
O. muricata auctt. *	Holland sand-dunes, Wood's Hole, Mass., and Orange, Conn.	ca. 10
O. ammophila Focke	Sand-dunes, Bremen (Germany), Heligoland, East Friesian Islands, and banks of the Elbe near Geesthacht.	11–15
O. germanica Boedijn	Rahnsdorf, near Berlin.	ca. 18
O. litorea Bartl.	Orange, Connecticut.	ca. 14
O. cruciata Nutt.............	Maine and Vermont to Mass. and N. New York.	10
O. Robinsonii Bartl.	Jaffrey, New Hampshire.	8
O. cleistantha Shull & Bartl. ...	Huntingdon, Long Island, N.Y.	10
O. atrovirens Shull & Bartl. = O. cruciata de Vries.	Hudson Falls (Sandy Hill), New York.	8–9
O. venosa Shull & Bartl.	Hudson Falls, New York.	ca. 10
O. eriensis Gates	Colchester, on shore of Lake Erie, Ontario.	9–15
O. novae-scotiae Gates	Annapolis Valley, Nova Scotia.	ca. 15
O. ammophiloides Gates & Catcheside.	Guysborough, Nova Scotia.	18
O. Victorini Gates & Catcheside.	St. Hubert, near Montreal.	26
O. parviflora L.	South Harpswell, Maine, and common near Washington.	5
O. Bauri Boedijn	Friedrichshagen bei Berlin.	ca. 20
O. pachycarpa Renner	Botanic Gardens of Munich and Jena.	10–13
O. campylocalyx Koch & Bouché.	Peru and Bolivia.	ca. 15

The following notes relate to species in the above Table :

O. erythrosepala Borbás.—Borbás (1903) has carefully described colonies of *Oenothera* near Budapesth. He describes *O. erythrosepala*, which differs from *O. grandiflora* in having a purplish stem, upper leaves with shorter petioles, and, especially, larger petals, which are subrotund-obovate, not emarginate or obcordate. *O. biennis* was also identified here, and a var. *pluriennis* which forms an innovation rosette. In its second season, after blooming it develops from the stem a rosette like that of the first year, which takes root in the late autumn. Another form, *O. hungarica*, is recognized, which resembles *O. muricata*. The name *O. purpurans* Borb. is given to natural hybrids between *O. erythrosepala* and *O. hungarica*. They are more like the latter, but are intermediate in flower-size. Here again is abundant evidence of natural crossing of species in a European population.

* The name *O. muricata* has been applied to this species by European authors. It has been called *O. syrticola* by Bartlett (1914 *b*).

It is worth pointing out that *O. grandiflora* has conspicuous basal lobes in the late rosette leaves.   In *O. novae-scotiae*, an unrelated species, similar rounded lobes are even more conspicuous, but only in the late rosette and early stem leaves.   The lobes often appear as a marked feature in hybrids of *O. novae-scotiae*, but they were not mentioned in the original description of this species.

O. Lamarckiana Ser.—A specimen in the Museum d'Histoire Naturelle in Paris, from seeds collected by Michaux (see photo in Gates, 1915, p. 72) in Eastern North America about the end of the eighteenth century apparently belongs nearer to *O. Lamarckiana* than to any other species.   The buds and ovaries are strikingly like those of *O. Lamarckiana* in form and pubescence, but are even larger in size.   The foliage, however, shows some marked differences from *Lamarckiana* and the pubescence is heavier.   As Davis (1927) concludes, this plant has no affinities with *O. grandiflora*.   It does show distinct and definite affinities to *O. Lamarckiana*, although the foliage differs.

O. multiflora Gates.—A study was made (Gates, 1914) of cultures from a colony near Birkenhead which contained *O. Lamarckiana* and *O. grandiflora*, their hybrids and a variety of derivatives, including four diverse types to which names were given.   *O. Lamarckiana* was also observed on Blundell Sands and in quantities at St. Anne's-on-Sea.

O. purpurata Klebahn.—Rudloff (1929) has shown that *purpurata* is, like *Hookeri*, homozygous and has seven free pairs of chromosomes in meiosis and practically all good pollen.   In the row of megaspores in *purpurata* both the uppermost and lowermost usually develop, thus generally producing two embryo sacs in the ovule.   Genetically *purpurata* is very similar to *Hookeri*, but differs markedly in having much smaller flowers.   This character behaves as a simple monohybrid difference in crosses with *Hookeri*, the small flower being dominant.   Renner (1929, p. 25) finds that in *Hookeri* × *purpurata* the flowers are distinctly smaller than in either parent, while in *purpurata* × *Hookeri* they are slightly smaller than in *purpurata*.   Thus, in addition to dominance of the small flower (and an absence of patrocliny) the *Hookeri* cytoplasm exerts an inhibiting effect on the flower-size.   There is other evidence as well that flower-size in hybrids is partly controlled by cytoplasmic differences.

O. Hewettii Ckll.—A segregate from *O. Hookeri*.   The buds are coloured as in mut. *rubrinervis*.

O. franciscana Bartl.—*O. franciscana* differs from *Hookeri* (Hoeppener & Renner, 1929, p. 55) only in having somewhat shorter, broader leaves and somewhat less red stem.

O. Jepsoni Greene ('Flora Franciscana', p. 211, 1891) is a small-flowered segregate apparently from *O. Hookeri*.

O. venusta var. *grisea* Bartl. differs from the species only in pubescence characters.

O. hirsutissima Rydb. is a segregate from the Californian *Hookeri*.   The latter has sepal tips 4 mm. long, the pubescence of the leaves is short, and not very copious on the calyx.   *O. hirsutissima* has sepal tips 2–2·5 mm. long,

the pubescence of leaves and calyx is long and loose, and is very copious on the calyx.

O. Jamesii Torr. & Gray.—The group of five species related to *O. Jamesii* agree in having large flowers which turn rose or purplish in drying. *O. irrigua* is similar to *O. Hookeri*, but much larger and more branched, with very different pubescence. *O. Jamesii* has much smaller flowers than *O. macrosiphon*, with abundant appressed canescently strigose pubescence, while *O. macrosiphon* has a stem hirsute with hairs arising from papillae and a very long hypanthium.

O. Clutei A. Nels. from Utah (Amer. Bot. 1922, xxviii, 22) is a segregate from *O. Jamesii* with smaller flowers.

O. longissima Rydb. differs from *O. macrosceles* in being canescent instead of glabrous and in having smaller and narrower bracts. It differs from *O. Jamesii* in being more canescent and less hirsute, and in having longer, narrower, and entire-margined leaves.

O. MacBrideae (Nelson) Heller is an erect, glabrate, herbaceous annual, with few flowers much larger than in *O. ornata*, which is a coarse, pubescent, spreading, very leafy biennial.

O. argillicola Mackenzie.—The three species *argillicola*, *levigata*, and *scitula* are all from the same type-locality, but *O. argillicola* is known to have a much wider distribution. The three are very similar in the rosette stage, but differ widely as they come into flower. *O. argillicola* shows certain similarities to *O. angustissima*.

O. rubricaulis Klebahn.—*O. rubricaulis* was found growing with *O. biennis*, *O. biennis sulfurea*, and *O. biennis cruciata* (Klebahn, 1914). Rudloff (1929) has shown that *rubricaulis*, like *O. biennis*, has a ring of six chromosomes and a ring of eight. It is strongly heterogamous, the complexes *tingens* ♀ . *rubens* ♂ corresponding to *albicans* . *rubens* of *O. biennis*. The chief character of the egg complex, *tingens*, as shown by many crosses, is the intensive red of the stem tip. This complex is represented in the pollen by shrunken, non-viable grains. The pollen complex is almost identical with that of *O. biennis*, and it carries larger flowers, while *tingens* carries determiners for small flowers and leaves.

O. numismatica Bartl.—This may represent a mutation from *O. pratincola*, as the latter in cultures produces a mut. *nummularia* with similar characters (Bartlett, 1915).

O. procera Wooton & Standl. is biennial or perennial, never branched. It differs from *strigosa* in having smaller flowers and different pubescence. *O. canovirens* is like *strigosa* in pubescence, but differs in characters of the flowers and fruit and in habit.

O. Cockerelli Bartl. is briefly characterized by de Vries (1913, p. 56, figs. 19, 20, 44, 45). It is near *O. strigosa* but has very small flowers, bluish green foliage, leaves with a long twisted tip. Renner (1925, p. 116) has determined its complex-formula as *curtans* . *elongans*.

O. subulifera Rydb. differs from *O. strigosa* in having sepals abruptly contracted into long subulate free tips.

O. depressa Greene is near *O. strigosa*, but prostrate, with broader, elliptical-lanceolate leaves, and much denser pubescence.   It is strongly annual.

O. brevicapsula Bartl. differs from *O. gauroides* in having short fruits and condensed spikes.

O. insignis Bartl.—A remarkable feature of *O. insignis* is that the lowermost fruits develop from the extreme base of the stem.

O. ammophila Focke.—*O. muricata* differs from this species in being more hairy and not having bent stem tips.   The differences are therefore slight, and *O. ammophila* has frequently gone under the European name *O. muricata* L.   Hoeppener and Renner (1928) have deduced from numerous crosses its formula *rigens*♀ . *percurvans*♂.   These terms refer to the erect or curved stem tip, which is more strongly bent (*percurvans*) in *O. ammophila* than in *O. muricata*.   *O. ammophila* also has more abundant red papillae on stem, ovary, and sepals.

O. germanica Boedijn has been shown (Hoeppener & Renner, 1928) to be almost identical with *O. ammophila*.   It should be regarded as not more than a variety of that species.

O. pachycarpa Renner.—This form is strongly heterogamous, like *O. muricata*, to which it is related, as indicated by its complex-formula *augens*♀ . *subcurvans*♂ (Rudloff, 1930).   He has also shown that it has a ring of fourteen chromosomes and two types of pollen grains, the larger with fusiform starch-granules, carrying the factor *subcurvans*, while the smaller inactive grains contain rounded starch-granules and bear the complex *augens*.

The various forms with cruciate petals are a very interesting series (Bartlett, 1914 *a*), some of them related to different ancestral species.   *O. cruciata* Nutt. was early recognized as an independent species.   *O. stenopetala* is clearly related to *O. Oakesiana*, while *O. stenomeres* is allied to *O. gauroides* and practically cleistogamous.   *O. Robinsonii* and *O. venosa* are both cruciate and nearly related, the former differing chiefly in having a smaller flower, more sharply dentate leaves, narrower bracts, and viscid pubescence of the buds. Other cruciate species are *O. atrovirens* and *O. cleistantha*.   *O. biennis* var. *leptomeres* is a cruciate variety of the European *biennis*.

In Table II (p. 190) are included the species whose genetic complexes or chromosome catenation have been investigated.   This makes it possible to develop much more definite conceptions of their relationships.

Much of the work represented in Table II has been done by Renner and his school.   The resulting analysis into complexes brings out relationships which would not otherwise be recognized.   Thus not only are similarities shown between the *acuens* complex of *O. grandiflora* and the *flavens* complex of *O. suaveolens*, but also between the *gaudens* complex of *O. Lamarckiana* and the *rubens* complex of *O. biennis*.   Moreover, the *albicans* complex of *O. suaveolens* and *O. biennis* are very similar but not identical, which suggests the derivation of one of these species through crossing with a third species.   *O. biennis* and *O. rubricaulis* similarly share the complex *rubens*, and their other complexes

(*albicans* and *tingens* respectively) differ but little. Further, the studies of Renner have shown that the complexes *velans*, *rigens*, and *Hookeri* have similarities indicating a common origin, while the complexes *curvans*, *percurvans*, and *flectens*, belonging respectively to *O. muricata*, *O. ammophila*, and *O. atrovirens*, are closely similar (see Hoeppener & Renner, 1928). Cleland (1931 *a*) has recently discussed further the relationships of these complexes, and shown that a model of these relationships corresponds in general with a model derived from the various catenations occurring in the species hybrids. He also points out that *O. suaveolens*, *O. biennis*, and *O. Hookeri* have been synthesized in crosses, and show the same catenation as the natural species.

Thus it seems clear that some of the cross-relationships and similarities between species must be accounted for by crossing between ancestral species, while some of the smaller differences between complexes of related species are due to gene mutations and some to interchange of chromosome segments. Parallel mutations, producing cruciate petals or smaller flowers in different lines of descent, represent another kind of phenotypic similarity, due to gene mutations. It is therefore important to note, from the systematic point of view, that gene mutations may produce in one case similarities and in another differences between species.

Some writers attempt to explain the evolution of the genus *Oenothera* purely by crossing, others by the process of segmental interchange of chromosomes in heterozygous forms, which Lotsy (1917) called internal hybridization. He refers to heterogamous species such as *O. Lamarckiana* or *O. biennis* as nuclear chimeras or heterogeneous syngameons, and to the production of partially or completely homozygous mutants from such species through chromatin rearrangements as intra-syngamic evolution. An example of the latter kind which could now be cited is the appearance of the half-mutant *rubrinervis* with four free pairs of chromosomes and a ring of six, from *O. Lamarckiana* with only one free pair and a ring of twelve. This means that segments of some of the chromosomes in the ring of twelve had undergone rearrangement so as to constitute three more homozygous pairs of chromosomes in fertilization. Similarly, *rubrinervis* in turn gives rise to *deserens*, which is completely homozygous and has seven free pairs of chromosomes.

It is clear, however, that both the processes of interspecific crossing and internal rearrangement of chromosome segments together are insufficient to account for all the multifold differentiation which has taken place in the genus in its North American habitat. Thus the cruciate condition of the petals has clearly arisen independently several times as parallel gene mutations in different lines of descent, to produce the cruciate species (many of them unrelated) *O. biennis* var. *leptomeres*, *O. stenopetala*, *O. cruciata*, *O. atrovirens*, *O. Robinsonii*, and *O. Heribaudi* (?). Crosses between these forms will ultimately determine in how far these mutations are strictly parallel, i.e. representing the same gene change in the same element of the germplasm in each species. Similarly, as already pointed out, there is evidence that dominant gene mutations

TABLE II.

	Complex-formula.	Author.	Chromosome catenation.
O. grandiflora	truncans, ♀; acuens, ♂.	Gerhard, 1929.	$(12) + 1_{II}$ † / (14)
O. suaveolens	(flavens, albicans), ♀*; flavens, ♂.	Cleland & Oehlkers, 1929, 1930.	$(12) + 1_{II}$
		Renner, 1919.	
O. Lamarckiana	(gaudens, velans), ♀; (gaudens, velans), ♂.	Renner, 1917 a.	$(12) + 1_{II}$
O. Hookeri	Hookeri (homozygous).	Hoeppener & Renner, 1929.	7_{II}
O. purpurata	purpurata (homozygous).	Rudloff, 1929 a.	7_{II}
O. franciscana	franciscana.	Hoeppener & Renner, 1929.	$(4) + 5_{II}$ or 7_{II}
O. biennis	(albicans, rubens), ♀; rubens, ♂.	Renner, 1919, 1925.	$(6) + (8)$
O. rubricaulis	tingens, ♀; rubens, ♂.	Rudloff, 1929.	$6 + 8$
O. Cockerelli	curtans, ♀; elongans, ♂.	Renner, 1919; Cleland & Oehlkers, 1930.	(14)
O. strigosa	deprimens, ♀; stringens, ♂.	Renner, 1925.	(14)

O. muricata..........	(rigens, curvans), ♀; curvans, ♂.	Renner, 1919, 1925.	14
O. ammophila	rigens, ♀; percurvans, ♂.	Hoeppener & Renner, 1928.	$12 + 1_{II}$
O. germanica	Almost identical with ammophila.	Hoeppener & Renner, 1928.	
O. atrovirens	pingens, ♀; flectens, ♂.	Renner, 1925.	
O. pachycarpa	augens, ♀; subcurvans, ♂.	Rudloff, 1930.	
O. angustissima	rubrans, ♀; divergens, ♂.	Gates & Catcheside, 1932.	14
O. pycnocarpa	dependens (dentans), ♀; dentans (dependens), ♂.	Gates & Catcheside, 1932.	14
O. nutans	serratans, ♀; nutens, ♂.	Gates & Catcheside, 1932.	14
O. erieneis	(undulans, glaucens), ♀; undulans, ♂.	Gates & Catcheside, 1932.	14
O. novae-scotiae	grandiflorens, ♀; parviflorens, ♂.	Gates & Catcheside, 1932.	14
O. chicagoensis	excellens, ♀; punctulans, ♂.	Renner (see Cleland & Blakeslee, 1930).	14

* About 80 per cent. of the embryo-sacs are *flavens* and 20 per cent. *albicans* (Hoeppener & Renner, 1929).

† This means a ring of 12 connected chromosomes and one free pair in diakinesis.

producing a decrement in length of the petal have occurred independently in various large-flowered ancestors in different parts of the American continent.*

The conception of parallel mutations, which was originally based on a case in *Oenothera* (Gates, 1912), is of the utmost importance, not only in this genus but in many others, and it is destined to receive much wider recognition in the construction of phylogenies. In addition to this class of mutations many other small and cumulative mutations must have occurred in the differentiation of the present swarm of frequently local *Oenothera* species. They are necessary also to account for many of the specializations and for some adaptations which have occurred in various species. As examples of the latter may be cited the canescent pubescence of *O. longissima* growing in xerophytic conditions and the prostrate habit, dense pubescence, and quick development as an annual of *O. depressa* living in a desert environment in Montana.

Writers who rely upon segmental interchange of chromosomes alone as an adequate basis for explanation of these remarkable specific specializations and adaptations develop a myopic point of view which sees only the narrower aspects of the problem. Thus, in order to make the facts fit his particular hypothesis of segmental interchange in *Oenothera*, Darlington (1931) finds it necessary to assume that *O. rubricalyx* has three pairs of chromosomes and a ring of eight, although it is well known that it has four pairs and a ring of six, like *rubrinervis*, from which it is a direct derivative as a dominant mutation (see Gates, 1915). The chromosome catenation of *O. rubricalyx* has been clearly demonstrated both in the microspore (Sheffield, 1927) and in the megaspore development (Gates & Sheffield, 1929). This mutant is in fact a direct proof, if such were needed, of gene mutation in *Oenothera*, in addition to such types as *brevistylis* and the various dwarfs, to say nothing of the gene mutations described by Shull (1921, 1928). An hypothesis which seeks to deny such well-established facts in the endeavour to show that 'all mutations in *Oenothera* depend upon segmental interchange of chromosomes cannot be taken very seriously, even although put forward with an elaborate array of subsidiary hypotheses.

A paper of Cleland (1931) suggests that the strain of *O. rubricalyx* ' Afterglow' which Shull obtained from Messrs. Sutton was perhaps pure *rubricalyx* in which segmental exchange of another pair of chromosomes had taken place, giving a ring of eight and three pairs. Whether this is so remains to be determined. The earlier form which Shull (1914) called *rubricalyx* was, however, certainly a hybrid with *O. grandiflora*, as shown by his own figures (see Gates, 1915 *b*) and also by the history of the material. In any case the proof remains, as before, that *O. rubricalyx* was derived from *O. rubrinervis* without any change of catenation.

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* From the various studies of flower-size inheritance there are indications that cytoplasmic differences between species also play a part in determining the flower-size in the hybrids.

SUMMARY.

In a discussion of the phylogeny of the subgenus *Onagra* of the genus *Oenothera*, based on genetical, morphological, cytological, and systematic results, it is indicated that *Onagra* was derived from the large-flowered subgenus *Raimannia*, probably in Central America, and that from this ancestry the small-flowered North American species were produced, through a series of dominant mutations, as the genus spread out and moved northwards following the retreat of the ice. The evidence for these conclusions is derived from (1) the present distribution of the small-flowered forms in America, (2) the conclusion that e.g. *O. Tracyi* is derived from *O. grandiflora* and *O. purpurata* from *O. Hookeri*, (3) the fact that occasional small-flowered mutations appear, e.g. *de Vriesii* and *bienniformis* from *O. Lamarckiana*, (4) the fact that *O. novae-scotiae* is composed of two complexes, *grandiflorens* and *parviflorens*, the former having petals much larger than the phenotype of the species.

Interspecific crossing has played an important part in the development of the subgenus, as a result of which most of the species are permanent crypthybrids, composed of two complexes and breeding true because of catenation or linkage of their chromosomes during meiosis. Thus the species with smallest flowers occur generally in the higher latitudes and usually show catenation of all their fourteen chromosomes into a closed ring. It has been shown experimentally that catenation can arise by crossing two homozygous species of *Oenothera* each having seven free pairs of chromosomes. Probably the hybrid vigour resulting from the heterozygous (heterogamous) condition leads to the survival and spread of such species, while the relatively homozygous derivatives which will occasionally arise through chromatin rearrangement in meiosis combined with inbreeding will be less likely to survive in the struggle for existence. This accounts for the fact that nearly all the small-flowered species show complete catenation.

Following the twin-hybrid results of de Vries, Renner and others have shown by extensive crossing experiments that most *Oenothera* species, including all which exhibit a high degree of catenation, are composed of two complexes, the phenotypic equivalents of which are often very different from the phenotype of the species.

The conception of parallel mutations in the subgenus is important, because of the evidence that dominant mutations giving rise to smaller flowers have appeared independently and successively in different parts of the continent from different lines of descent. The species and varieties with cruciate petals constitute another series of independent parallel mutations.

The large amount of specialization and adaptation in some species of *Oenothera* can only be adequately accounted for by the accumulation of small germinal changes (mutations), many of which must have taken place to account for the amount of specific differentiation which appears in the genus. That gene

mutations occur is known from the existence of such Mendelian mutants as *brevistylis, rubricalyx* and the various dwarf types.

Interchange of segments between non-homologous (heterogamous) species, called by Lotsy internal hybridization or intra-syngamic evolution, will account for the appearance of a certain number of new types, especially those which are more nearly homozygous than the parent form ; but so far as known these usually fail to survive in competition with the more heterozygous, and hence more vigorous, species from which they are derived. For these and other reasons the value of segmental interchange as an evolutionary factor is limited in comparison with the importance of interspecific crossing. Such crossing probably took place on a large scale in the early evolution of the group, producing a swarm of crypthybrids with a high degree of chromosome catenation, which were successful in spreading on account of their hybrid vigour. Gene mutations occurring regularly throughout this swarm are sufficient to account for the further differentiation of species which has taken place, segmental interchange of chromosomes playing a minor rôle in the same forms.

Two new species are described, and the recognized species of subgenus *Onagra* are listed, with their type-localities, petal length, and indications of their relationships and chief differences. The complexes and chromosome catenation are also given in those species in which it has been worked out, and references are made to various studies of naturalized hybrid populations in Europe.

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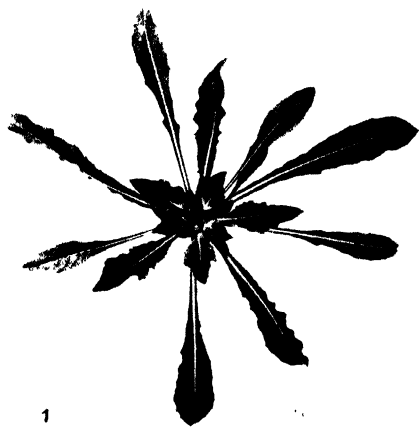
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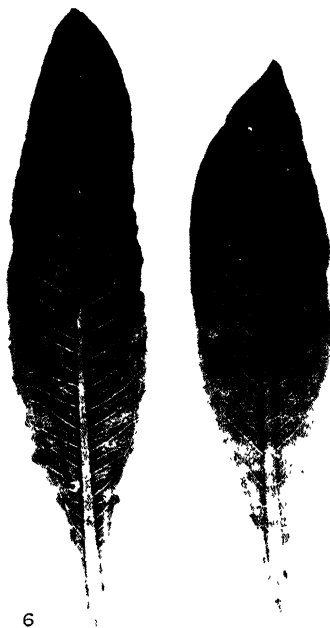
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EXPLANATION OF PLATE 26.

Fig. 1. *Oenothera ammophiloides.* Young rosette.

Fig. 2.   „   „   Two rosette leaves.

Fig. 3.   „   „   Oblique flowering stem.

Fig. 4.   „   „   Shoot in fruit.

Fig. 5. *O. Victorini.* Young rosette.

Fig. 6.   „   Two rosette leaves.

Fig. 7.   „   Flowering shoot.

Fig. 8.   „   Shoot in fruit.

The cause of petaloid colouring in ' Apetalous ' Flowers. By EDITH R. SAUNDERS, sometime Fellow of Newnham College, Cambridge.

IT is a familiar fact that of those Dicotyledon types which have but a single perianth only a minority have the members of this whorl green and herbaceous after the manner of typical sepals.   In the great majority of monochlamydeous types the perianth is coloured—more rarely it is white.   The colour may be due either to the sap or the plastids.   It may be exhibited over the whole of both surfaces, or it may be chiefly or entirely confined to the inner face or to the margins.   When white, the absence of colour is usually total, though in some cases tinting of the marginal region of each perianth member may be observed. Or, again, only the margins may be white, the middle region remaining green.

The class with *green* sepal-like perianth members includes, with certain exceptions*, the families of the Chenopodiaceae, Moraceae, Urticaceae, and Ulmaceae, and scattered genera in various other families, among which may be cited the Amarantaceae and Polygonaceae, and the parasitic Loranthaceae and Santalaceae.

The many types in which the single perianth is *petaloid* are distributed over a very much wider range of families.   These include the monochlamydeous families of the Proteaceae containing some fifty genera, Nyctaginaceae and Aristolochiaceae.   Certain genera in the Amarantaceae, Phytolaccaceae, and Santalaceae; many in the Aizoaceae.   The small families of the Myristicaceae, Penaeaceae, Geissolomaceae and Oliniaceae, and the monochlamydeous section of the larger family of the Thymelaeaceae.   To this list, which does not claim to be complete, must be added numerous acyclic or hemicyclic genera in the Ranunculaceae ; some monochlamydeous genera which occur as exceptions in certain typically dichlamydeous families such as Sterculiaceae, Leguminosae, and Sarraceniaceae ; probably, several species of *Nepenthes*.

The question has frequently arisen in the past whether the members of the single perianth (conveniently indicated by the term tepals) are to be regarded in this or that case as corresponding with the sepals or the petals of the 2-whorled perianth.   Nevertheless, no principle of general application for the determination of this point has hitherto been formulated.   It may be added that the accepted interpretation cannot in many cases be regarded as beyond doubt.   The examination of the whole floral anatomy of a large number of widely distributed genera, undertaken in the first instance with other objects in view, has, however, brought to light the existence of a definite relation between

* See later, p. 209.

colour development and the vascular scheme of the perianth. This relation would appear to point the way to a principle of general application, enabling us to determine the true morphological nature of the tepal in each individual case.

In order that the full significance of the anatomical feature commonly distinguishing the green and non-green type of single perianth, respectively, may be appreciated, it will be necessary to consider for a moment the general vascular scheme of the Dicotyledon type possessing both calyx and corolla, and having the full number of whorls, with the full number of members in each whorl. In such a perfect cyclic type, which we will here suppose to be pentamerous, we might expect on general grounds to observe the following series of events. That at the flower base groups of elements in the central vascular cylinder would become organised on five equidistant radii into five bundles, which would turn out from the central cylinder and become the midribs of the outermost floral whorl—the sepals. That after their departure a second set would turn out in the same manner on the five alternate radii and become the midribs of the second floral whorl—the petals. That these would be followed again by a third set of bundles which would turn out on the same radii as the sepals and pass to the outer stamens. That a fourth set, on the same radii as the petal set, would similarly run to the inner stamens. That a fifth set on the original radii would become the midribs of the outer carpels. That a sixth and last set, on the alternate radii, would pass to the fertile carpels, the whole of the vascular tissue being used up in the course of these appropriations. It is probable, however, that these several stages are never all to be seen *as so many separate events* in any one species. The shortening of the floral axis, which is generally supposed to have taken place in cyclic types, necessitates some modification which will result in a certain measure of speeding-up, and economise space. This need has been met by condensing some stages in the above series, two or more outgoing bundles becoming associated together and leaving the central cylinder simultaneously as 'one trunk cord, instead of successively as so many separate strands. This 'condensation' process may involve association of adjacent strands *belonging to different radii*, as when a strand proper to a sepal radius is conjoined for a longer or shorter distance with another strand proper to an adjacent petal radius. Or a lower set of strands issuing on one set of radii may carry out conjoined with them another set of strands *proper to these same radii*, but destined for a later (=higher) superposed whorl. As examples of the first case—that of lateral union—we may cite the numerous instances in which the strands which become the marginal veins of the sepals are not given off as branches from the sepal midribs, but take their rise direct from the central cylinder. When this is the case the ten marginal veins usually issue conjoined in pairs as five trunk cords, each cord dissociating later into the right marginal vein of the adjacent sepal on the one side and the left marginal vein of the neighbouring one on the other side. When the sepal marginals are combined in pairs in this way, they carry out conjoined with them a third component—the midrib bundle for the petal on that radius, sometimes even

a fourth component—the bundle for the superposed stamen, the departure of these midrib bundles being somewhat hastened, we may suppose, by this arrangement. Again, we meet with cases, notably among the Leguminosae, where the ten strands which give rise to the midribs of the five sepals and five petals arise as five, six, or seven trunk-cords which shortly dissociate into their component bundles, these bundles then taking up their position on their proper radii. In contrast with these examples of what we may term *lateral* ' condensation ' are those in which this process takes place in the *vertical* direction, as when, for example, the bundles for the stamens are carried out conjoined with the midrib bundles of the perianth members upon which they are superposed. The normal regular alternation of the several whorls is bound up with, and rests upon, the out-turning of the vascular strnds for each successive whorl on the radii alternating with those proper to the strands of the preceding whorl. If the strands for the members of two superposed whorls are conjoined into a single set of trunk cords, the two whorls are treated as one by the next succeeding whorl. It is therefore easy to understand how it can come about that the inner of two such conjoined whorls may become suppressed without affecting the position of the following whorl, for the number and position of the outgoing strands will remain unchanged. It is through recognition of this direct relation between the vascular ground-plan and the floral ground-plan—a relation which is fundamental and universal—that we are enabled to arrive at a satisfactory explanation of the floral scheme, whatever the particular method of ' condensation ' adopted, without having recourse to the wholly groundless assumptions required in many instances in order to meet the facts. The primulaceous flower affords a familiar case in point. In order to account for the superposition on the petals of the single staminal whorl in this family, it has been suggested by some writers that the obviously normal petals and the equally obviously normal stamens are not really the members of two distinct whorls, but represent a single whorl which has undergone tangential splitting. Whereas the simple explanation here, as in innumerable other comparable cases, is that the bundles for the two superposed whorls have arisen as trunk cords which dissociate after leaving the central cylinder into petal and stamen components. The same form of ' condensation ' is characteristic of a large section of the Monochlamydeae, in which the members of the single stamen whorl do not alternate with, but are superposed upon, the members of the single perianth (Moraceae, Urticaceae, Ulmaceae, Chenopodiaceae*). In these cases the difficulty has either been passed over (Moraceae, Urticaceae, Chenopodiaceae), or recourse has been had to explanations which, as in the Primulaceae, can only be described as morphological fictions (Ulmaceae). In *Ulmus* and in the allied genus *Holoptelea*, for example, the superposition of the stamens on the tepals has been accounted for on the supposition that the five (or more) perianth-segments really represent the surviving members of *two theoretical*

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* In many Chenopodiaceae the staminal bundles are now in process of disappearing or have already been lost.
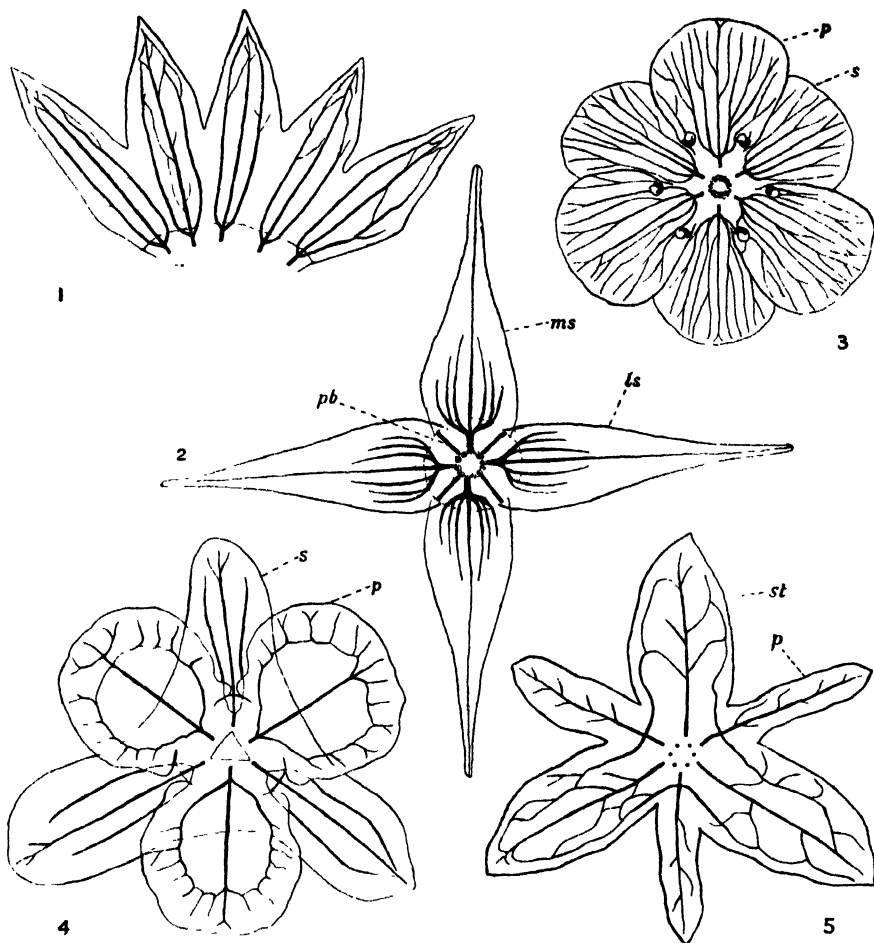
Fig. 1.—*Melochia nodiflora* Sw. (Sterculiaceae). Dichlamydeous, cyclic, pentamerous type. The gamosepalous calyx split down one suture and laid flat ; below a torn piece of the axis. The sepals with midrib and true lateral veins.

Fig. 2.—*Epacris longiflora* Cav. (Epacridaceae). Dichlamydeous, cyclic, tetramerous type. The floral axis with the polysepalous calyx pressed flat, viewed from above. The four orthogonal sepals with midrib and true lateral veins. On the alternate radii the bundles for the four petals which have been removed. In the centre the residual vascular ring.

Fig. 3.—*Cabomba aquatica* Aubl. (Nymphaeaceae). Dichlamydeous cyclic type, with trimerous flowers. The floral axis with calyx (almost completely polysepalous) and corolla pressed flat, viewed from above. The sepals, like the petals, with true lateral veins derived from the midrib.

Fig. 4.—*Rumex* sp. (Polygonaceae). Dichlamydeous cyclic type, with trimerous flowers. The floral axis with calyx (gamosepalous at the base) and corolla pressed flat, viewed from above. Sepals as well as petals with true lateral veins.

Fig. 5.—*Emex spinosa* Campd., ♂. Dichlamydeous cyclic type, with trimerous flowers. The floral axis with the 2-whorled perianth pressed flat. The three large outer perianth members with midrib, and commissural marginal veins at first conjoined with the midrib bundles of the smaller inner members. Within the axis the bundles for six stamens.

ls, lateral sepal ; *ms*, median sepal ; *p*, petal ; *pb*, petal bundle ; *s*, sepal.

whorls (3). In this way it is suggested that the superposed stamens can be looked upon as occurring in proper alternation with the tepals. Not only is there no foundation for such an assumption, but it is wholly unnecessary. In *Ulmus* the perianth segments, whatever their number, arise simultaneously, the perianth-stamen trunk cords all leave the central cylinder at the same level. In *Zelkova* it is true that the two median tepals arise at a lower level than the 3–6 others on the other radii, which all arise simultaneously. There is no hint here, however, of any time-difference which can be regarded as the outcome of a 2-whorled ground-plan, the above deformation of the perianth being simply due to the much greater development of the young gynoecium in the median as compared with any other plane. Nor does the fact that in *Holoptelea integrifolia* Planch. the stamens are sometimes more numerous than the tepals furnish any support to the assumption that the perianth is 2-whorled. If, when dissociation of the perianth-androecium trunk cords takes place, it should happen that the bulk of a particular cord becomes detached to furnish the stamen bundle, so that only a feeble strand remains for the tepal, that particular tepal may fail to take shape. The resulting floral ground-plan would then be exactly such as is found in individual flowers of *Holoptelea*. This explanation was, in fact, regarded by Bentham and Hooker (2) as more probable than that the supernumerary stamens represented members of an incomplete second staminal whorl. It has seemed necessary to deal thus at length with the Ulmaceae since, if the interpretation hitherto adopted be pushed to its logical conclusion—if, that is to say, the perianth, which has clearly the character of a single perianth, is nevertheless to be regarded, even though theoretically, as being double—there would be a certain contradiction in listing this family among the Monochlamydeae, although this anomaly seems to have been ignored by those accepting this interpretation.

At this point we must leave discussion of those cases where 'condensation' takes place in the vertical direction, since in the further consideration of our present subject we shall need to concern ourselves more particularly with the most usual example of lateral 'condensation' cited above, in which the marginal veins of the sepals leave the central cylinder conjoined with the petal midribs.

This vascular arrangement is of wide-spread occurrence. It would seem, in fact, to be far more common than that in which the sepal marginal veins arise as true lateral veins from the sepal midrib (text-figs. 1–5). As the sepal-petal trunk cords make their way to the periphery the petal midrib bundles become detached, each passing into the corresponding petal as it becomes exserted. The remaining portion of the trunk cord destined for the calyx sooner or later divides in two. In a polysepalous calyx the two resulting strands immediately diverge, the one passing to the sepal on the right, the other to that on the left. In a gamosepalous calyx the calyx component of the trunk cord may remain undivided for a considerable distance, only splitting in two just below the level at which the sepal-segments become free. Such a calyx shows in the gamosepalous region single commissural veins alternating with the·
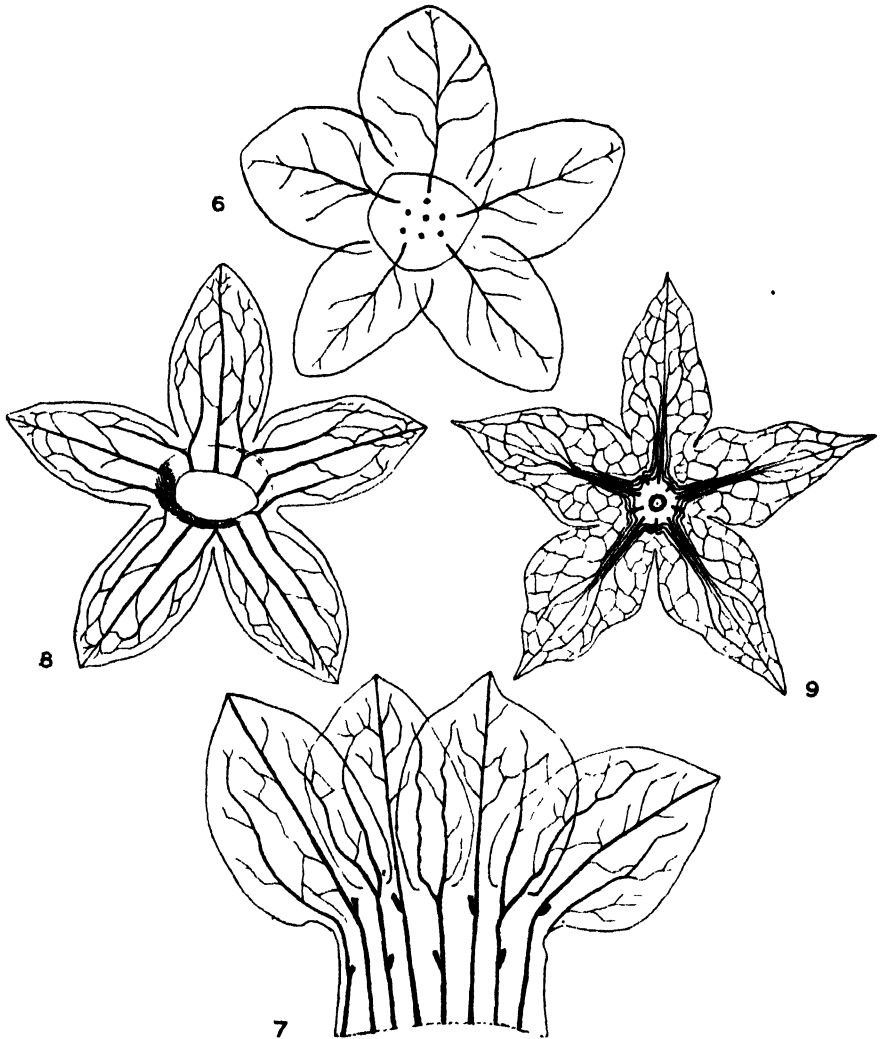
Fig. 6.—*Muehlenbeckia chilensis* Meissn., ♂ (Polygonaceæ). Flower from which the stamens have been removed, viewed from below. The five tepals with midrib and true lateral veins. In the centre the bundles for six stamens in a ring round a central strand which shortly comes to an end.

Fig. 7.—*Daphne Mezereum* L. (Thymelaeaceae). Monochlamydeous, cyclic, tetramerous type, with gamophyllous petaloid (coloured) perianth. Upper portion of the perianth tube split down one commissure, laid open, and pressed flat. Tepals with commissural marginal veins conjoined at first with the stamen bundles on these radii, later becoming free, ultimately forking just below the level at which the tepals become disjoined. [For simplicity the anthers have been removed. The non-vascular outgrowths at the mouth of the tube are also not shown.]

Fig. 8.—*Cola acuminata* Schott & Endl. (Sterculiaceae). Monochlamydeous, cyclic, pentamerous type, with petaloid (coloured) perianth. The partly gamophyllous perianth viewed from above. The tepals with midrib and commissural marginal veins. [The marginal veins arise as trunk-cords conjoined at first with the stamen bundles on these radii. After disjunction they take up a position about half-way between the midrib and the edge.

Fig. 9.—*Thomasia solanacea* J. Gay (Sterculiaceae). Monochlamydeous, cyclic, pentamerous type, with petaloid (white) perianth and non-vascular petal rudiments. The floral axis with the perianth, viewed from above. The tepals with midrib and commissural marginal veins. [The marginal veins, which arise as in *Cola* (fig. 8), come to lie alongside the midrib.]

midribs *. These two forms of commissural venation are well seen in the Caryophyllaceae, in the polysepalous Alsinoideae and gamosepalous Silenoideae, respectively (6).

When we examine the vascular anatomy of genera possessing only a single perianth, we find that these monochlamydeous types can be grouped, like dichlamydeous forms, into two classes. In the one class we shall include those types in which each perianth member receives only a midrib bundle, any secondary veins which may be developed arising from this bundle as true lateral veins (text-fig. 6) ; also those types with separate marginal veins *when these veins spring from elements lying alongside the midrib-bundle elements in the central cylinder*. To the other class will belong the forms in which each perianth member receives in addition to the midrib bundle half the commissural bundle lying on the alternate radius on each side (text-figs. 7–9) ; and, as well, those in which the marginal veins arise separately both from the midrib and from each other *when these veins spring from elements in the central cylinder lying not in those sectors containing the perianth midrib bundles but in the alternate sectors* (text-figs. 10–13). A comparative study of these two classes has brought to light the significant fact that in those monochlamydeous forms in which the vascular system of the perianth consists solely of the vascular elements turning out from the central cylinder on one set of radii or sectors, the perianth is green like the sepals of a typical calyx. On the other hand, in those forms in which the perianth members receive vascular strands belonging to both sets of radii or sectors—midrib bundles lying on what we may term the sepal radii and commissural marginal bundles derived from trunk cords or from separate strands on the alternate or petal radii or sectors, the perianth very generally exhibits some degree of petaloid colouring. It may be added that in the Monochlamydeae the presence or absence of commissural marginal veins appears to be a character which runs through the whole of a genus, whereas in the Dichlamydeae it may vary from species to species (observed in the Primulaceae)

* Whether such temporary association of the petal midribs with the sepal marginals produces any direct modification of the calyx character is a question needing further investigation.

TEXT-FIG. 10.
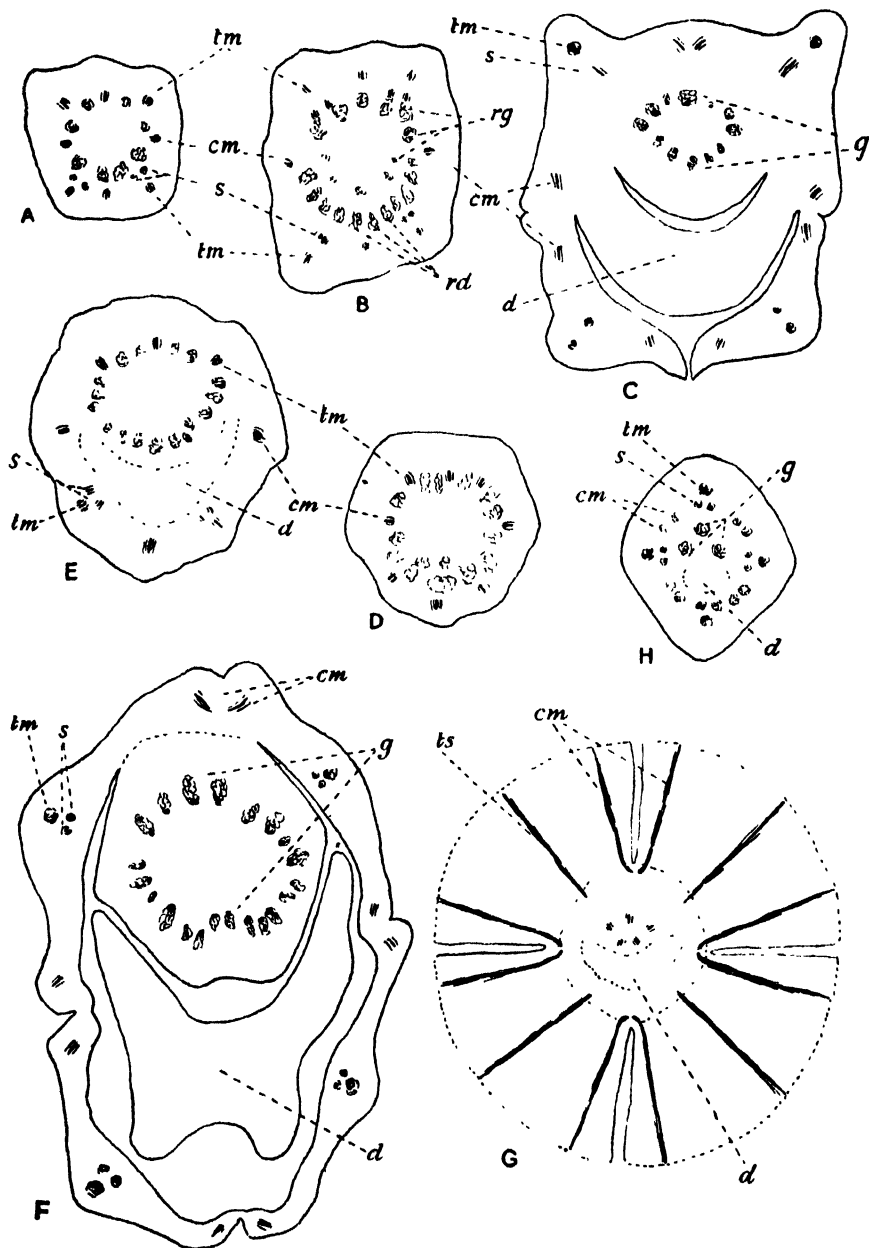
Grevillea spp. (Proteaceae). A–C, *G. punicea* R. Br. A. Flower base. The bundles for the four diagonal tepals are seen issuing from the central vascular figure at the corners, those for the commissural marginals as trunk-cords from the middle of each side. B. The same after the above-mentioned eight bundles for the perianth have left the central vascular figure. On the diagonal radii twin strands abutting on the gaps

left between the central vascular bundles by the departure of the perianth midrib bundles are turning outwards, each pair fusing later to become a single stamen bundle. Nearer the centre on the lower side a half circle of residual vascular elements which pass to the glandular disc and the front half of the gynoecium. C. The flower at the level at which perianth, glandular disc, and ovary are becoming disjoined. The four tepals with midrib, commissural marginals, and the superposed bundle for the stamen. Above the disc the partially free gynoecium with a symmetrical vascular figure showing a median bundle back and front. D–F. *G. bipinnatifolia* R. Br. D. Flower base at a slightly earlier stage than that shown in A. E. The same at a stage between those shown in B and C. F. The flower at a slightly later stage than that shown in C. G. *G. Thelemanniana* Hueg. The flower at the level of exsertion of the tepals. The two components of each commissural trunk cord are diverging in order to furnish the marginal veins of the corresponding tepals. H. *G. glabrata* Meissn. Flower base. In this species the ovary and glandular disc stand in line with the median tepal midribs in contrast with the preceding species in which the plane of symmetry passes through two of the commissural trunk cords. Owing to the small number of vascular strands (three) entering the ovary, and to the fact that the glandular disc appears to be without vascular elements, the allocation of the vascular bundles to tepals, stamens, and carpels is rapidly completed. [All from transverse sections.]

d, disc ; *cm*, commissural marginal veins ; *g*, gynoecium bundles ; *rd*, residual vascular elements for the disc ; *rg*, residual vascular elements for the gynoecium ; *s*, stamen bundles ; *tm*. tepal midrib bundle.

(6) and, possibly even, from individual to individual.* A list of monochlamydeous types † in which the colour and venation of the tepals have so far been examined is given below.

List of monochlamydeous types examined in which the green tepals are without commissural marginal veins, ‡ any secondary veins which are present being derived by branching from the midrib.

Cyclic types.

Chenopodiaceae ... *Chenopodium* spp., *Beta* spp., *Hablitzia tamnoides* Bieb.
Urticaceae .... *Parietaria officinalis* L., *Pellionia Daveauana* N. E. Br., *Urtica* spp., *Villebrunea integrifolia* Gaudich., *Pilea* spp.

* That this should be the case is not surprising, seeing that in the monochlamydeous type the character involved is a fundamental feature in the plan of construction ; variation here would often mean the whole difference between the formation and the total suppression of an outgoing perianth strand on the one set of radii. Whereas in dichlamydeous types an outgoing strand will always be formed on this set of radii to provide the midribs for the petals ; variability here will merely be a matter of disjunction or non-disjunction of some elements from these strands.

† For our present purpose *Asarum, Thomasia*, and *Gnidia* may be included in this category, since generally in the first two genera, and often in the last-named, the structures representing a corolla are small non-vascular remnants.

‡ I have deliberately used the term 'marginal' in referring to these veins of commissural origin, since to describe as 'lateral' veins which do not spring from the midrib would introduce ambiguity and obscure the present issue. These commissural veins are truly marginal in so far that they lie nearer to the margin than any of the other prominent veins, but they do not necessarily lie close to the edge but may take up any position between margin and midrib,

Moraceae	*Humulus japonicus* Sieb. & Zucc.
Ulmaceae	*Celtis australis* L., *C. occidentalis* L., *Ulmus* spp., *Zelkova acuminata* Planch., *Z. crenata* Spach.
Amarantaceae	*Amarantus* spp.
Santalaceae	*Osyris abyssinica* Hochst., *Thesidium fragile* Sond.
Loranthaceae	*Viscum album* L.
Phytolaccaceae....	*Petiveria alliacea* L.
Cornaceae	*Garrya elliptica* Dougl.

Hemicyclic and acyclic types.

Polygonaceae	*Muehlenbeckia chilensis* Meissn., *M. complexa* Meissn., *M. axillaris* Walp.

List of monochlamydeous types examined in which the petaloid tepals have commissural marginal veins.

Cyclic types.

Proteaceae	*Diastella serpyllifolia* Salisb., *Grevillea bipinnatifida* R. Br., *G. glabrata* Meissn., *G. oleoides* Sieber, *G. punicea* R. Br., *G. rosmarinifolia* A. Cunn., *G. Thelemanniana* Hueg., *Leucadendron adscendens* R. Br., *L. Stokoei* Phillips, *Leucospermum Hypophyllum* R. Br., *Mimetes lyrigera* Knight, *Protea mellifera* Thunb., *Serruria* sp., *Spatalla* sp.
Nyctaginaceae	*Boerhavia* sp., *Bougainvillea* sp., *Mirabilis Jalapa* L. *Abronia umbellata* Lam., *Oxybaphus glabrifolius* Vahl.
Aristolochiaceae ..	*Aristolochia Clematitis* L., *A. Pistolochia* L., *A. rotunda* L., *Asarum caudatum* L., *A. europaeum* L.
Amarantaceae	*Achyranthes argentea* Lam., *Celosia* sp., *Gomphrena* sp.
Penaeaceae	*Brachysiphon speciosus* Sond., *Penaea mucronata* L., *Sarcocolla squamosa* Kunth.
Geissolomaceae....	*Geissoloma marginatum* Kunth.
Oliniaceae	*Olinia cymosa* Thunb.
Thymelaeaceae ...	*Daphne Laureola* L., *D. Mezereum* L., *D. pontica* L., *D. buxifolia* Vahl, *Gnidia carinata* Thunb., *G. pinifolia* L., *Lachnaea* sp., *Peddiea Dregei* Meissn., *Pimelia ferruginea* Labill., *Phaleria Blumei* Benth.
Aizoaceae	*Aizoon sarmentosum* L., *Glinus* sp., *Tetragonia* spp.
Santalaceae	*Colpoon compressum* Berg., *Thesium capitatum* L., *T. humifusum* DC., *T. resedioides* A. W. Hill.
Phytolaccaceae....	*Ledenbergia rosea-aenea* Lem., *Rivina humilis* L.
Sterculiaceae......	*Brachychiton populneum* R. Br., *Cola acuminata* Schott & Endl., *Fremontia californica* Torr., *F. mexicana* Macb., *Sterculia (Firmiana) platanifolia* L., *S. alata* Roxb., *Thomasia quercifolia* J. Gay, *T. solanacea* J. Gay.

Leguminosae . . . . . .   *Saraca indica* L.
Myristicaceae . . . . .   *Myristica fragrans* Houtt.
Sarraceniaceae . . . .   *Heliamphora nutans* Benth.
Nepenthaceae . . . .   *Nepenthes* sp.

Hemicyclic and acyclic types.

Ranunculaceae . . .   *Clematis Flammula* L., *C. Thunbergii* Steud.

Of the monochlamydeous types listed above *all those in which there are no lateral veins in the tepals, or in which such lateral veins as are present arise either by branching from the midrib after it has left the central cylinder or spring direct from vascular elements in the central cylinder lying alongside those giving rise to each midrib* (Petiveria), *the perianth is green.* On the other hand, *all those which are furnished with marginal veins of commissural origin* (with perhaps the exception of some species of *Nepenthes*) *exhibit some measure of petaloid colouring.* From these facts we obtain an insight into the proximal cause of the green or non-green appearance of the single perianth where this is strictly a tepal characteristic (see later, p. 215). It must, however, be made clear that, owing either to effect of environment or to some quality inherent in the constitution of the species, this relation between tepal colour and tepal vascular anatomy may in some types be completely masked. The following instances will serve as illustrations. Members of the family Urticaceae have in most cases a green perianth, but in a plant of *Urera baccifera* Gaudich. growing under 'stove' conditions the perianth was observed to be tinted with anthocyanin, although the tepals were without marginal veins. Again, in an individual of *Procris frutescens* Blume (another member of this family) growing under the same conditions the tepals were greenish white, although without other veins than the midrib. Now in the *Urera* plant it was the case that not only was the perianth tinted but the axis of the inflorescence and the pedicels were coloured a deep red, even the ovary was slightly reddish. Here the flooding with anthocyanin, owing to some quite distinct cause, of the whole region of the inflorescence, tepals included, entirely masks such green colouring of these latter members as is to be expected from their vascular anatomy. Similarly, in *Procris* the greenish white colouring is not here a *tepal* characteristic due to tepal anatomy *but is a general feature of the inflorescence axis and pedicels.* The same is the case in *Chenopodium purpurascens* Jacq., in which the flooding with anthocyanin is even more extensive than in *Urera*. In short, in none of these apparently anomalous cases do we find genuine exceptions to the general rule given above.

Exceptions illustrating the converse condition, in which, though the vascular anatomy would lead us to expect petaloid colouring, such colouring is absent, may equally be expected. Some species and hybrid forms of *Nepenthes* would appear to come under this head. Examination of the flowers of the hybrids *N. formosa* Veitch and *N. mixta* Mast. showed the presence of commissural marginal veins in the perianth (text-fig. 12), yet the flowers in these two forms
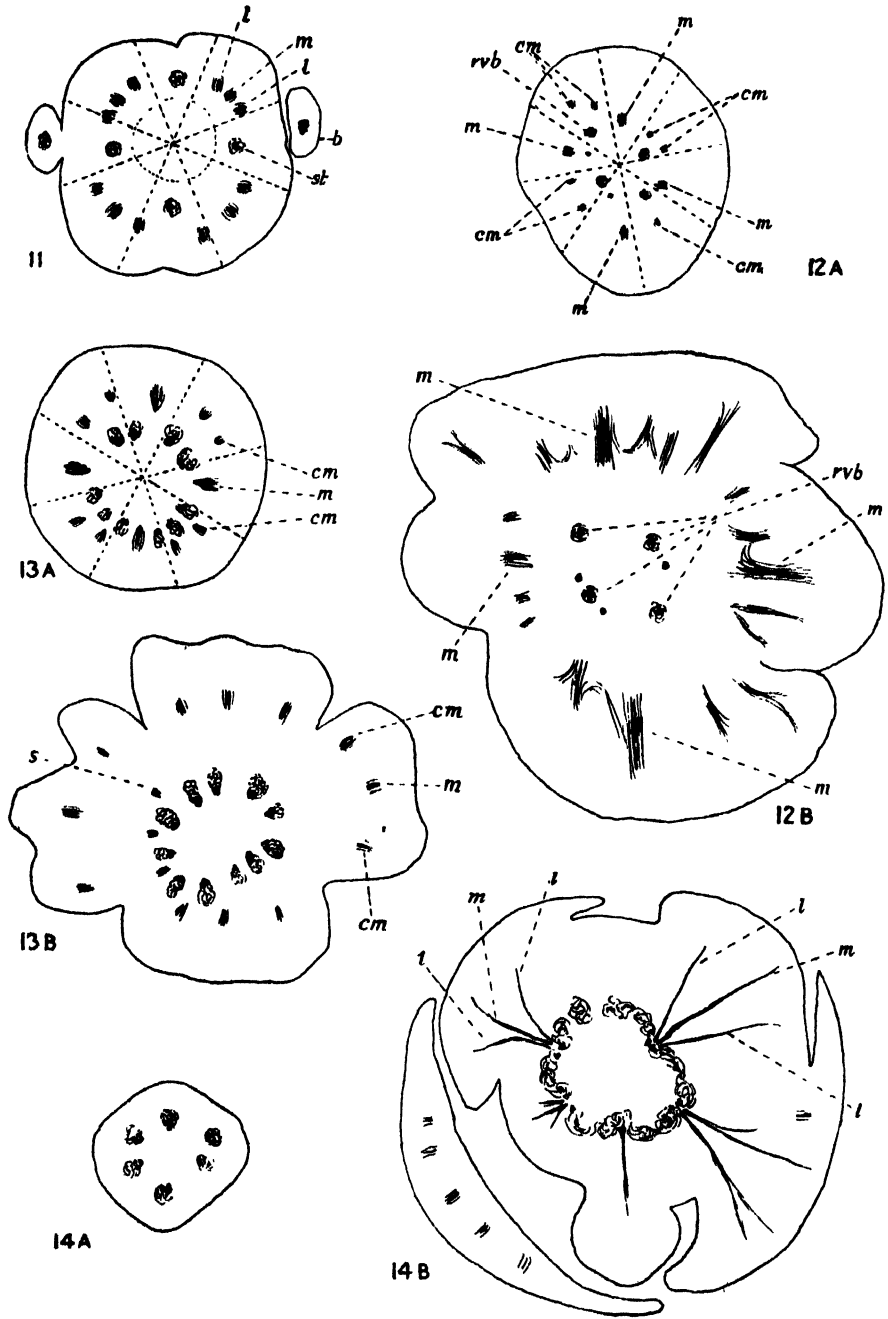
Fig. 11.—*Petiveria alliacea* L. (Phytolaccaceae). Flower base. In the four diagonal sectors the midrib and marginal bundles of the four tepals. Somewhat nearer the centre on the alternate (orthogonal) radii the bundles for four stamens. To right and left the bracteoles not yet completely exserted. Below, in the centre line, the depression in the outline at the junction of two tepals marking the position of the bract (not shown) already exserted. [The vascular elements for the gynoecium are not represented.]

Fig. 12.—*Nepenthes mixta* Mast. (Nepenthaceae), ♂. A. Flower base just above the level of emergence from the central cylinder of the midrib and marginal bundles of the four tepals. The marginal veins originate separately from the midribs and in the sectors alternating with them. In one case (below on the right) the commissural trunk cord has not yet become resolved into its two components. Nearer the centre four residual bundles which supply the stamens. B. The same at a higher level showing early anastomosis between the commissural marginal veins and the midrib bundles of the tepals.

Fig. 13.—*Clematis Flammula* L. (Ranunculaceae). A. Flower base showing the emergence of the tepal midribs in the orthogonal sectors and that of the commissural marginal veins in the diagonal sectors. B. The same at a higher level. The four tepals can now be distinguished, each with midrib and two marginal veins. In the centre the residual vascular ring from which the bundles for the stamens are beginning to emerge.

Fig. 14.—*Anemone Hepatica* L. (Ranunculaceae). A. The pedicel of a young flower bud immediately below exsertion of the perianth. B. The flower bud just above the level of exsertion of the outermost tepal showing anastomosis between the bundles of the central cylinder. The marginal veins of the tepals spring direct from the central cylinder, arising from elements lying alongside those which give rise to the midrib bundles. [All from transverse sections. In 11, 12 A, and 13 A the sepal and petal sectors are indicated by unlettered dotted radial lines.]

b, bracteole ; *cm*, commissural marginal bundles ; *l*, lateral bundle ; *m*, midrib bundle ; *rvb*, residual vascular bundle ; *st*, stamen bundle.

were green. Now since, as previously stated, the commissural vein character appears usually to be constant for the genus among the Monochlamydeae, we may suppose that such veins are present in other (? all) species of *Nepenthes*. This is rendered almost certain by the fact that several species are known which, unlike the two forms mentioned above, have the tepals more or less petaloid. Thus in *N. Curtisii* Mast. they are green with white margins ; in *N. distillatoria* R. Grah. the inner face is tinged at the edges with purple ; in *N. Rafflesiana* Jack the whole inner surface is deep purple, while the outer face is green. Here we see the petaloid feature which, if our supposition regarding the vascular anatomy is correct, we should expect. It may be that in those types with wholly green tepals the physiological constitution of the plant is such that it is unable to develop petaloid colouring under the particular conditions of its habitat.*

* Unfortunately living flowers of coloured species have not so far been obtainable for examination and comparison. It has not therefore been possible to ascertain whether the unusual occurrence of anastomoses between midrib and commissural marginals, which takes place in the two above-mentioned garden forms before the tepals are exserted, may result in a weak petaloid characteristic becoming suppressed owing to a counteracting sepaline influence.

That individual species may be so constituted is well seen in a dichlamydeous type in *Deherainia smaragdina* Decne. (Myrsinaceae), in which the calyx is succeeded by a large corolla as green as the leaves. It must, in fact, be recognised that though petaloid colouring, when a purely tepal feature, is directly conditioned by tepal vascular anatomy, a visible outcome of this relation will depend upon its being a physiological possibility.

Among the types cited in the above list those belonging to the Phytolaccaceae are of special interest, since here we have three closely related genera, in all of which the tepals receive marginal veins originating separately from the midribs, yet the perianth of one (*Petiveria*) is green* while that of the other two is petaloid, being coloured throughout in *Ledenbergia*, and being white, with or without tinted margins, in *Rivina*. This difference (between a green and a non-green appearance) is entirely in accord with the difference in vascular ground-plan. The marginal veins in *Petiveria* are derived from elements in the central cylinder lying alongside those which give rise to the midribs—that is to say, from elements in the sepal sectors (text-fig. 11), while the corresponding veins in *Ledenbergia* and *Rivina* originate in the petal sectors (7).

The inclusion in the foregoing list of plants of some species belonging to the Thymelaeaceae (*Daphne Laureola* L., *D. pontica* L., *Peddiea Dregei* Meiss.), in which the flowers are greenish yellow or yellowish green, needs a word of explanation. Although in most species of *Daphne* the flowers are either coloured with anthocyanin or are white, one species at least is known in which the flowers are of a golden yellow (*D. Giraldii* Nitsche). Some others have flowers which are distinctly yellow though much paler (*D. linearifolia* Hart). Now in these species the perianth colour is due to full yellow and pale yellow plastids, respectively. It only needs slight further variations in the same direction to produce the greenish yellow and yellowish green appearance in the three species cited above. There can be little doubt that just as the red- and purple-flowered species differ in the depth of colouring those which owe their colour to the plastids vary in a similar manner, and that the petaloid feature which we see in full measure in *Daphne Giraldii* is manifested, but in descending scale, in *D. linearifolia*, *D. pontica*, *D. Laureola*, *Peddiea Dregei*, and other members of the Thymelaeaceae.†

Certain features occurring in two other genera listed above, viz. *Gnidia* and *Saraca*, also call for further brief comment. Various species of *Gnidia* possess

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* Paling later to white. This change, however, affects also bract and axis and is not strictly, therefore, a tepal characteristic.

† Since the green appearance of the angiosperm leaf is due, as we believe, to a mixture in the plastids of both green and yellow pigments, it will be readily understood that if in the yellow flowers of a series of species the additional yellow plastid pigment which produces an appreciable petaloid coloration of the tepals should be present in successively decreasing amounts, it may become difficult to determine by mere inspection when this petaloid component reaches vanishing point. All that concerns us here, however, is that in *D. Laureola*—the lowest member in the series cited above—that point is definitely not reached.

structures at the mouth of the flower tube alternating with the perianth seg-
ments. These structures, which in some species are completely non-vascular,
and in others receive a portion of the trunk cord on the corresponding radius,
evidently represent petal remnants, and to this extent *Gnidia* is not strictly
a monochlamydeous type. In order to account for the position of these petal
structures it has been generally held in the past that the flower tube is formed
of an extension of the receptacle. This assumption is entirely at variance with
the vascular anatomy and is unnecessary on the present view that in the
Thymelaeaceae generally the flower tube is wholly a perianth-stamen tube,
receiving on the one set of radii the trunk cords for an outer perianth whorl
and superposed stamens, and on the other set of radii the trunk cords for the
outer perianth marginals and an inner perianth whorl with superposed stamens,
though the stamens, sometimes, and the petals, still more often, no longer
attain their full individual development. In species where no vascular petal
structures are developed, each trunk cord on these radii, after giving off the
strand for the superposed stamen, becomes used up as it forks to furnish
a marginal vein to the outer perianth member on either side. Hence these
members may properly be termed tepals. Where *vascular* rudiments of petals
occur the scheme is similar except for the additional branch running to these
structures.

Saraca indica L. shows the exceptional condition among the Leguminosae
of a single perianth of four cruciform subequal members which are somewhat
thick and coloured. The scheme of distribution of the bundles to the perianth
members is here entirely different from that of the other types cited in the above
list, for *Saraca*, despite its tetramerous perianth, is fundamentally a pentamerous
type like most members of the Leguminosae. No one of the four tepals
corresponds with any of the five sepals or five petals of a typical member of the
Caesalpineae. As I have elsewhere described (4), ten separate bundles leave the
central cylinder for the perianth as in typical dichlamydeous members of the
family. But whereas in these latter types one of the ten bundles runs to each
of the ten perianth members, in *Saraca* three bundles pass into each member
of one pair of tepals and two into each of the other two members. Thus each
perianth member receives one or, in one case, two of the bundles proper to the
petal radii, hence their petaloid colouring. One may safely predict that the
same distribution of the perianth bundles as that seen in *Saraca* will be found in
the allied genus *Apalatoa*, in which the four members of the single perianth
are membranous, and in *Hardwickia* and *Copaiba* in which they are petaloid.

Before dealing with certain considerations of a more general nature, passing
mention may be made of a genus of the Aizoaceae constituting a category by
itself, viz. *Mesembryanthemum*, which is usually described as possessing a single
perianth and having on the several alternate radii an outer group of petaloid
staminodes and an inner group of stamens. Now the stamen and staminode
groups on any one radius are both served by strands *derived by copious branching
from a single trunk cord on that radius*. It is thus clear that the staminodes
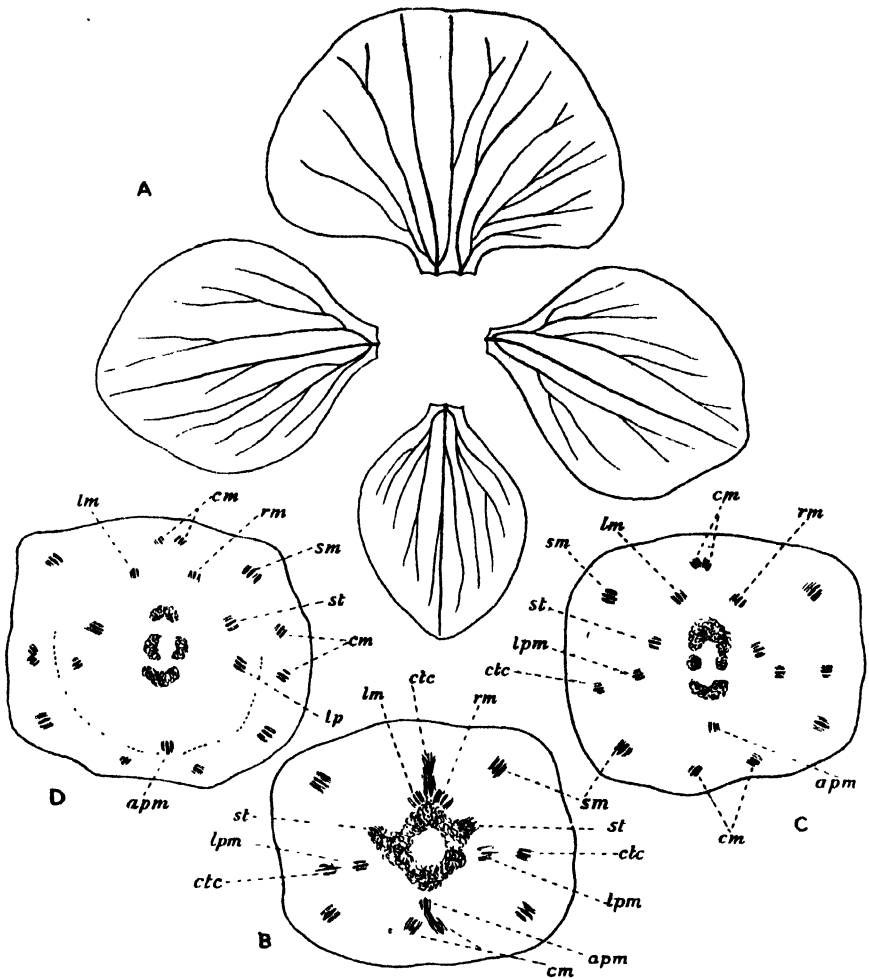
Veronica pectinata L. (Scrophulariaceae). A. The four petals isolated. The anterior
and lateral petals each with a single midrib bundle, the posterior petal with two midrib
bundles. B–D. Transverse sections of the flower base taken from below upwards.
B. Towards the periphery in the diagonal planes the midrib bundles of the four sepals ;
in the orthogonal planes the trunk cords which become dissociated into the commissural
marginals for the sepals and the midrib bundles for the petals. The development
of twin midrib bundles in the posterior petal is already indicated. The anterior cord
has already forked to furnish the marginal veins for the adjacent half of the two
neighbouring sepals ; the remaining portion is becoming detached to provide the petal
midrib. Around the pith a ring of young vascular elements from which the bundles
for the two stamens are becoming differentiated and can already be identified as they
begin to emerge. C. The same after the bundles for sepals, petals, and stamens have
all become distinct except that the two lateral commissural bundles have not yet
forked. In the centre the vascular strands for the gynoecium not yet fully differentiated.
D. The same after the bundles for all whorls are differentiated. The calyx ring
is now partly defined and shows the midrib and two marginals of each sepal.

apm, anterior petal midrib ; *cm*, commissural marginal bundles ; *ctc*, commissural trunk
cord ; *lm*, left midrib bundle of the posterior petal ; *lpm*, lateral petal midrib ;
rm, right midrib bundle of the posterior petal ; *st*, stamen bundle.

are petaloid, *because they receive the component of the trunk cord which in a typical dichlamydeous form would enter a petal*. Both the petal component and the staminal component of the cord break up into numerous strands, so that in place of a single petal and single superposed stamen a group of petaloid staminodes and a superposed group of stamens are formed.

It will be evident from what has gone before that the tepal of monochlamydeous types cannot be regarded as having the same morphological equivalence in all species. In those without commissural marginal veins, the single perianth members clearly correspond with the sepals of a dichlamydeous type. In those in which commissural marginal veins are present the individual tepals, though having equally the outward appearance of unit structures, are, in fact, structurally compound. Where the whole of the perianth vascular component of each perianth-stamen trunk cord on the petal radii passes into the tepals, half to the adjacent one on the right and half to the corresponding one on the left, and where no non-vascular rudiments of petals remain, the individual tepal may be looked upon as the counterpart of a sepal bordered on either side by half a petal—that is to say, it may be considered as equivalent to $\frac{1}{2}1\frac{1}{2}$ of the radially disposed units of which monochlamydeous and dichlamydeous flowers alike are constructed. It may be that it will remain the custom to apply the term tepal indifferently to the members of any single perianth whether they represent simple or compound structures. Indeed, any other course scarcely seems practicable. For in addition to such clear-cut cases as those above-mentioned standing at either end of the scale, we meet with various intermediate grades in which, although the perianth vascular component on the petal radii is diverted to furnish commissural marginal veins to the perianth members on the sepal radii, non-vascular outgrowths representing petal rudiments still survive, as in *Thomasia* (Sterculiaceae), *Asarum* (Aristolochiaceae), species of *Gnidia* (Thymelaeaceae). It is essential, however, that the different character of the structures denoted by the term tepal should be appreciated if we are to arrive at an understanding of various problems presented by the single perianth.

The existence of a form of tepal representing the outcome of development on $\frac{1}{2}1\frac{1}{2}$ radii—in other words, corresponding to $\frac{1}{2}1\frac{1}{2}$ members of the double perianth—recalls the mode of splitting with which we have long been familiar in the androecium of the Fumarioideae. More recently the conception of carpel polymorphism has shown us that such splitting is a common feature of the gynoecium, particularly in the fruiting stage. The present investigation makes it clear that in the gamophyllous monochlamydeous type with commissural marginal veins similar splitting takes place when the tepals become disjoined. The process leading to the formation of the $\frac{1}{2}1\frac{1}{2}$ compound structural unit is thus seen to be of common occurrence and to occur among all types of floral members.

The facts set forth in the preceding pages lead to the conclusion that certain perianth characteristics, which we may briefly distinguish as sepaloid and petaloid, are generally laid down in the cyclic flower in definite relation to the two alternate sets of radii on which such flowers are constructed. This localisation of

certain features along certain radial construction lines can be traced back to, and is bound up with, the vascular ground-plan, and is independent of whether, or how, the perianth is cut up into segments. Attention was first directed to an example of such lack of relation between the ground-plan of the corolla and certain anatomical features of the petals by W. and A. Bateson in their account of the floral variations exhibited by certain species of *Veronica*. These authors found the colour pattern in these forms to be laid down in definite relation to certain radii, apparently without regard to the scheme of segmentation (1). I have since shown that in *Lobelia Erinus* L. both the colour pattern and marginal ciliation are similarly fixed in relation to the radii and are independent of the particular scheme of segmentation (5). The tetramerous corolla of *Veronica* is held to have been derived from a pentamerous type by the fusion of the members standing in the postero-lateral planes. This is *inferred* from various facts, but it can actually be *demonstrated* by means of the vascular ground-plan. For in some tetramerous species (e.g. *V. pectinata* L.) the posterior member of the corolla receives *two* midrib bundles which give rise to two distinct systems of venation. This was found to be the case also in *V. satureioïdes* Vis., a species with five sepals, and we should expect that other penta-sepalous species will show the same construction. These systems remain distinct throughout (text-figs. 15 A–D). This feature is evidently not connected with the size of the corolla, for in *V. gentianoides* Vahl, with larger flowers than *V. pectinata* L., only a single midrib was found in the few flowers examined. Moreover, in some species, as e.g. *V. filiformis* Sm., the flowers with one midrib and those with two appear to be about equally abundant. Both conditions were also observed in *V. cinerea* Boiss & Bal.*

In hemicyclic and acyclic flowers the direct connection between colour development in the perianth and the position in respect to the radii of the point of origin of the perianth bundles is less obvious than in cyclic types, the vascular scheme being of a less stereotyped character in the former as compared with the latter class. Nevertheless, in a number of species which have been examined the connection was plainly traceable. In certain types in which the perianth members are few and definite in number, forming a whorl in an otherwise acyclic flower as in species of *Clematis* (text-fig. 13), or where the perianth members are variable in number but do not occupy more than the two turns of a spiral which would correspond to a single whorl in a pentamerous type, as in *Heliamphora nutans* Benth., the perianth members are furnished with a midrib and marginal veins which are not true lateral veins. These marginal veins spring direct from the central cylinder, the two of a pair being separated sometimes from each other and from the midrib bundle which they accompany by portions of the residual vascular cylinder destined for the androecium and gynoecium. These marginal veins are, nevertheless, strictly commissural in origin here as in certain cyclic types such as the Proteaceae (see text-fig. 10),

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* It is proposed to deal further with this character in a separate communication.

for they originate at points within the petal sectors, the difference between such types and most cyclic forms being merely that in the latter the radii can generally be treated as linear, whereas in acyclic types such as the above they are to be regarded as sectorial. Comparison of numerous examples of both cases shows that the result (as regards colouring) is the same at whatever point halving of the vascular component of the petal sector takes place, whether at the earliest moment when the elements still form part of the central cylinder, or as late as possible, when the trunk cord formed by these elements as they leave the central cylinder approaches the level of disjunction of the tepals.

In *Anemone,* in which the tepals are usually numerous, the method of introducing the petal colouring is different again. Here the marginal veins of the tepals are always, so far as experience goes, produced by true lateral branching from the outgoing midrib bundles. But at the moment of origin of the midribs a sudden horizontal anastomosis takes place between the vascular elements of the central cylinder allocated to these midribs and those which occupy the intervening sectors and will remain behind, a form of anastomosis which is peculiar to this level and does not occur later when the stamen and carpel strands are formed (text-fig. 14). Hence it seems reasonable to suppose that by this anastomosis the same effect is accomplished as by the formation of separate individual marginal, but not true lateral, veins as in *Clematis,* or by trunk cords as in most cyclic types. Other variations in the fundamental vascular scheme by which the same end is attained doubtless occur, but sufficient examples have been given to illustrate the nature of the connection between the vascular ground-plan and the colouring of the single perianth. We may then summarise the points which have emerged from the preceding considerations as follows.

SUMMARY

The typical dichlamydeous cyclic Dicotyledon is so organised that the petaloid character of the corolla can be regarded as a function of a certain combination of conditions as regards time and space : time, in so far that the petaloid feature occurs at a definite stage in the series of developmental processes, following, as it does, upon the differentiation of a (usually) uncoloured (i.e. green) calyx ; space, in that it is exhibited on the set of radii alternating with the radii of the sepals. Penetrating a little below the surface appearance, we find we can express these same relations in terms of the vascular anatomy as follows. Those floral members (again taking the typical case) which receive as midribs the first set of equidistant bundles to leave the central cylinder show sepaloid characters ; those similarly receiving as midrib bundles the outgoing strands on the alternate set of radii exhibit petaloid colouring.

It is found that the marginal veins of the sepals of such Dicotyledon types arise in two different ways, less frequently as true lateral veins from the midribs, more often either through the detachment from the central cylinder on the alternate radii of trunk cords which dissociate in due course into a petal midrib

and twin bundles which enter the adjacent side of the sepal to right and left, respectively, and become the marginal vein of that side; or through the departure of pairs of separate strands within the limits of the corresponding alternate sectors.

In typical monochlamydeous cyclic Dicotyledons radial organisation follows the same scheme as in dichlamydeous types, notwithstanding that the perianth here takes the form of a single whorl of structures. Such monochlamydeous types may be divided into two classes. In the one class only the issuing vascular bundles on the corresponding set of radii enter the perianth members. These bundles become the midribs. They may give off lateral veins at any point or may remain unbranched. *In either case the individual member is homologous with the individual sepal and is typically green.* In the other class each member receives not only the bundle on its own radius but also half the perianth component proper to the alternate radius on each side, either as separate strands or (in gamophyllous types) as undisjoined components of perianth-stamen trunk cords. The first-mentioned bundle becomes the midrib of the tepal, the two others become marginal veins, the one entering the tepal on the right, the other that on the left. *In forms belonging to this class the tepals are typically petaloid. Each may be regarded as the counterpart of one sepal of dichlamydeous types + half the neighbouring petal on either side.* This equivalence is not infrequently indicated outwardly by the considerable thickness of the tepal members as compared with that of the sepals and petals of the nearest allied dichlamydeous forms.

The accompanying drawings were made by Miss D. F. M. Pertz, to whom I desire to express my grateful thanks.

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Diatoms (recent and fossil) of the Tay district. By DAVID McCALL, B.Sc.,
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    Prof. F. E. FRITSCH, D.Sc., Ph.D., F.L.S.)

(With a Map and 38 Text-figures)

[Read 18 February 1932]

THE present paper is the result of an attempt to prepare as complete a list as
possible of the Diatomaceae occurring in the district of the Tay Estuary.
The materials for these investigations were collected during the years 1921–25.

The district of the Tay Estuary is particularly favourable for a study of the
Diatomaceae, as, within a tract of country twenty-seven miles long and sixteen
miles broad, there are sea-coast, sandy shore, meadow-lands, and uplands :
a large river runs through the area : there is a difference in altitude from
sea-level to 1,500 feet. Marine, brackish, lowland freshwater, sub-alpine, and
alpine species are all well represented.

The diatoms of the Sidlaw Hills are particularly interesting, as here are
found such ‘ relicta ’ forms as *Navicula gibbula* Cl., ,and *N. Semen* Ehb.
Hustedt (21), referring to *N. gibbula*, says : ‘ The discovery of this species in
the Sarek Mountains is one of the most interesting finds of the present work.
It has hitherto only been found in the arctic regions, in Greenland, Franz
Joseph's Land, Spitzbergen, Beer's Island, and Jan Mayen. The fact that it
has been found in all the arctic freshwater materials which have been investi-
gated confirms the assumption that it is widely distributed in these regions,
although apparently sparsely. Hitherto it was unknown south of the Polar
Circle—therefore, it is of interest to find it here. Especially noteworthy is the
fact that I have recently found it in a soil sample from the Jarvens Lilltrask
in the south of Finland. Doubtless we must conclude that it exists here as
a glacial relic.’ That this diatom should occur in the living state at Rait,
Invergowrie, and Liff, in the Tay district, is therefore of considerable interest.
Of *Navicula Semen* Cleve (2) says : ‘ *N. Semen* seems to be a northern species,
rarely found living, but frequently in post-glacial deposits of Scandinavia and
North America. It is not mentioned by Brun as an inhabitant of the Alps
nor by Belloc as occurring in the Pyrenees. Its occurrence in the living state
in the Harz is an interesting fact, and suggests that it may be a survival from
the post-glacial epoch.’ This diatom occurs in the living state in Laird's Loch,
Tullybaccart (Sidlaw Hills) at an altitude of 900 feet.

As the district affords ample evidence of severe glaciation, as shown by the
moulding of the hills and by the deposits of boulder clay, sands, and gravels,
the finding of these diatoms is noteworthy. There is every reason to believe
that they are relics of the post-glacial epoch.

The following species found in the area are usually considered to be northern or alpine species :—

Navicula gibbula Cl.

N. Semen Ehb.

Caloneis obtusa W. Sm.

C. alpestris Grun.

C. Silicula v. *alpina* Cl.

Cymbella heteropleura Ehb.

C. incerta Grun.

C. incerta v. *naviculacea* Grun.

The following sub-alpine species are also found in the area :—

Pinnularia lata Breb.

P. alpina W. Sm.

P. divergentissima Grun.

Neidium bisulcatum Lagerst.

Anomoeoneis exilis Grun.

A. brachysira Grun.

Cymbella Cesatii Rabh.

C. angustata W. Sm.

Melosira distans Kütz.

The genus which is most poorly represented is *Mastogloia*. Only in one locality—Quarry Pond, Invergowrie—is the genus well represented, *M. elliptica* v. *Dansei* being abundant there.

The marine species were obtained in various collections made at Carnoustie, Easthaven, and Tayport, and in collections made with a silk tow-net (160 mesh) at various places in the Tay Estuary.

The fossil forms were obtained from the raised beach exposed at Invergowrie, Longforgan, Errol, and Glencarse. The raised beach contains two well-marked layers of clay, the upper yellowish, sandy, and containing practically no diatoms ; the lower consisting of blue clay and containing over forty brackish and marine species. (See note, Loc. 39.)

The diatoms were collected from an area of about 250 square miles, bounded on the north by a line extending from Pole Hill eastwards along the Sidlaws to Monikie and Easthaven, and on the south by a line running from Tentsmuir westwards to Lindifferon and Dunbog and including Dura Den. From this area over one hundred collections were made, most of them during the spring and autumn maxima, and from these collections over one thousand strewn slides were prepared and systematically examined. Before the collections were cleaned they were examined for the purpose of determining their general nature, the other organisms present, and the presence or absence of auxospores. No attempt was made to investigate cytology or reproduction, as it was felt that these points could only be satisfactorily dealt with after a systematic study of the group had been made and a knowledge of distribution had been obtained. It is rather remarkable that although over nine hundred species

and varieties have been found in the area, only twenty-one species showed auxospore formation. In one of these—*Diatoma hiemale* Heib.—auxospore formation was hitherto unknown. The following table gives some idea of the relative frequency of auxospore formation as observed in the different species :—

Cymbella ventricosa	in	six	collections.
C. cistula	,,	three	,,
C. aspera	,,	three	,,
C. parva	,,	two	,,
Gomphonema olivaceum	,,	three	,,
G. lanceolatum	,,	one	,,
G. subclavatum	,,	one	,,
G. constrictum	,,	one	,,
Amphora ovalis	,,	three	,,
Epithemia zebra	,,	two	,,
E. turgida	,,	two	,,
Frustulia vulgaris	,,	two	,,
Neidium affine	,,	one	,,
Pinnularia divergens	,,	one	,,
Navicula viridula	,,	one	,,
N. cryptocephala	,,	two	,,
N. peregrina	,,	two	,,
Caloneis amphisboena	,,	one	,,
Nitzschia sinuata	,,	one	,,
Surirella biseriata	,,	one	,,
Diatomale hiemale	,,	two	,,

The majority of the collections containing auxospores were gathered from the end of March to the middle of May, although a few were obtained in November, and one (*Diatoma hiemale*) in late February. The present list contains 920 species and varieties, of which a number are new records for Britain, and a few are new species or varieties.

Part of the work for this paper was carried out in the Botany Department, Dundee Technical College. The author gratefully acknowledges help received from Miss Helen S. Ogilvie, M.A., B.Sc., in connection with the plankton of the Tay.

LIST OF LOCALITIES

(Map ; Ordnance Survey of Scotland, Sheet 24.)

Loc. 1. Scraped from the surface of mud left by receding water round the edges of the pool near the Ice House, Tentsmuir.

Principal species :—*Navicula anglica* Ralfs, *Achnanthes lanceolata* Breb.

Loc. 2. Floating masses srom grouse drinking hole, Tentsmuir. The diatoms were associated with a pale yellowish-green alga—*Cladophora flavescens* Ag.

Prin. sp. :—*Synedra familiaris* Kütz. Not found elsewhere in the district.

Loc. 3. Long, brown, filamentous strands from fast-running water in burn, Tentsmuir.

Prin. spp. :—*Fragilaria capucina* Desm., *F. intermedia* Grun., *F. virescens* Ralfs., *Synedra acus* Grun., *S. ulna* v. *danica* V. H., *Diatoma elongata* Ag.

This collection contains the rare diatom *Navicula pusio* Cl.

Loc. 4. Floating reddish-brown masses detached from the mud in ditch by the production of air bells, due to active photosynthesis, Shanwell, Tentsmuir.

Prin. sp. :—*Cymbella naviculiformis* Auers.

Loc. 5. Ditch containing a large amount of iron bacteria (*Leptothrix ochracea*), near Morton, Tentsmuir.

Prin. sp. :—*Nitzschia obtusa* v. *Schweinfurthii* Grun. This species makes up about 90 per cent. of the collection.

Loc. 6. Boggy pools near Morton, Tentsmuir.

Prin. spp. :—*Pinnularia major* Kütz., *P. nobilis* Ehb., *P. gentilis* Donk., *Navicula bacillum* Ehb.

Map of localities.

Loc. 7. Scraped from the surface of mud at edge of Morton Lochs, Tentsmuir.

Prin. spp. :—*Cymatopleura elliptica* W. Sm., *C. solea* W. Sm. (rather small forms).

Loc. 8. A collection of diatoms from the surface of mud under the banks of a stream which flows into the Tay at Tayport. The water is brackish, as the stream is within tidal influence. The collection contains marine, brackish, and freshwater forms, the latter, e.g. *Gomphonema geminatum*, having been brought down by the river. There are about 220 forms in the collection.

Prin. spp. :—*Pleurosigma balticum* W. Sm., *P.* spp. (various), *Surirella fastuosa* Ehb., *Amphiprora* spp., *Nitzschia* spp., *Coscinodiscus* spp. ·

Loc. 9. Brownish film lying in sand ripples near high water, Tayport.

Prin. spp. :—*Navicula digito-radiata* v. *Cyprinus* W. Sm., *N. cancellata* Donk., *N. humerosa* Breb.

Loc. 10. From sand ripples and small pools exposed at low tide, near Tayport.

Prin. spp. :—*Surirella gemma* Ehb., *Navicula digito-radiata* v. *Cyprinus* W. Sm., *Actinoptychus undulatus* Ehb.

Loc. 11. Brown filamentous masses attached to hydrophytes in pond, Chesterhill, near Tayport.

Prin. spp. :—*Fragilaria capucina* Desm., *Diatoma elongata* Ag., *Synedra ulna* Ehb., *Navicula viridula* Kütz., *N. cryptocephala* Kütz.

Loc. 12. Floating aerated masses in pond, Chesterhill.

Prin. sp. :—*Navicula cryptocephala* Kütz. The only species present.

Loc. 13. Greyish-brown granular masses from bottom of shallow pool, Scotscraig, Tayport.

Prin. spp. :—*Navicula oblonga* Kütz., *Fragilaria pinnata* Grun., *Synedra ulna* Ehb.

Loc. 14. Forgan Bog. The diatoms were collected from the stream at one end of the bog, and from the water amongst the rushes. A very rich collection, containing about 150 forms (species and varieties), the greater number of which are freshwater species, but a few are acknowledged brackish forms. *Navicula radiosa* Kütz. is particularly abundant, whilst the closely related form *N. viridula* Kütz. is very scarce. *Amphipleura pellucida* is also abundant. There is a variety of *Cymbella aspera* which is much beyond the maximum size given by Cleve and other authors, some specimens reaching a length of 350 μ. This I have named v. *gigas*. The genus *Pleurosigma* is not represented. The collection from this locality bears a very close resemblance to several collections from the Sidlaws (1,100–1,400 feet), many boreal and sub-alpine species being common to both localities.

Loc. 15. Dura Den. Scraped from Old Red Sandstone rocks under waterfall.

Prin. spp. :—*Epithemia argus* Kütz., *E. argus* v. *longicornis* Grun.

A number of abnormal forms of the above occur, which are post-auxospore forms.

Loc. 16. Gelatinous masses from the surface of wet rocks in quarry, St. Fort Estate.

Prin. spp. :—*Cymbella parva* W. Sm., *Nitzschia sinuata* Grun.

Contains abnormal forms of *N. sinuata* (post-auxospore forms).

Loc. 17. Scraped from sides of iron boiler in field behind Woodhaven.

Prin. spp. :—*Synedra ulna* Ehb., *Cymbella parva* W. Sm., *C. ventricosa* Kütz.

Loc. 18. Diatoms epiphytic on algae attached to rocks, exposed at low tide, Woodhaven.

Prin. spp. :—*Cocconeis scutellum* v. *stauroneiformis* W. Sm., *Melosira Jurgensii* Ag., *Synedra investiens* W. Sm., *Rhabdonema arcuatum* Kütz., *R. minutum* Kütz., *Actinoptychus undulatus* Ehb.

Loc. 19. From mud and stones in Motray Water.

Prin. spp. :—*Navicula* spp., *Nitzschia* spp., *Synedra* spp., *Cymbella* spp.

Loc. 20. Filamentous masses scraped from the sides of an iron boiler below water spring, on the beach above high-water mark, Balmerino.

Prin. spp. :—*Diatoma vulgare* Bory, *Fragilaria construens* Grun., *Synedra affinis* Kütz.

Loc. 21. From surface of rocks, Balmerino Harbour.

Prin. spp. :—*Synedra affinis* v. *fasciculata* Kütz., *Navicula viridula* Kütz., *Rhoicosphenia curvata* Grun., *Nitzschia* spp.   .

Loc. 22. From pools, Balmerino Harbour.

Prin. spp. :—*Amphipleura rutilans* Trentepohl, *Synedra affinis* v. *fasciculata* Kütz.

Loc. 23. Dark brown gelatinous masses on surface of mud, below shallow still water, beside weir, Kilmany.

Prin. sp. :—*Cymatopleura solea* W. Sm.

Loc. 24. From pond filled with *Equisetum*, near Lindifferon, Luthrie.

Prin. spp. :—*Navicula cryptocephala* Kütz., *N. viridula* Kütz., *Nitzschia amphibia* Grun., *N. palea* W. Sm., *N. communis* Rabh., *Meridion circulare* Ag., *Surirella ovata* Kütz., *Achnanthes lanceolata* Breb.

Loc. 25. Scraped from stones in burn near Lindifferon, Luthrie.

Prin. spp. :—*Gomphonema olivaceum* Kütz., *Navicula cryptocephala* Kütz., *N. viridula* Kütz.

Loc. 26. A collection of diatoms obtained by scraping a floating plank in canalised stream, west of ditch leading from the Brick and Tile Works, Glencarse, to River Tay. The water is brackish. This accounts for the mixture of marine, brackish, and freshwater forms found in the collection. The total number of forms is about 120.

Prin. spp. :—*Nitzschia* (*Homoeocladia*) *filiformis* W. Sm., *N. fasciculata* Grun., *Navicula peregrina* Kütz., *Surirella pyriformis* Kitt.

Loc. 27. Brownish film scraped from the surface of mud exposed at low tide, Port Allen. A rich collection containing marine, brackish, and freshwater forms—in all about 75 species.

Prin. spp. :—*Navicula peregrina* Kütz., *Caloneis amphisboena* Bory, *Pleurosigma* spp., *Diploneis* spp., *Coscinodiscus* spp.

Loc. 28. Scraped from stones and mud, at low tide, around the dyke, between Seaside and Errol.

Prin. spp. :—*Navicula viridula* Kütz., *N. mutica* f. *Cohnii* Hilse.
Contains the somewhat rare *N. bahusiensis* Cl.

Loc. 29. From marshy ground amongst rushes near Seaside.

Prin. spp. :—*Navicula peregrina* Kütz., *Nitzschia plana* W. Sm., *Surirella pyriformis* Kitt.   .

Loc. 30. Scraped from the sides of iron boiler used as a drinking trough and from surface of mud beside the boiler, Seaside.

Prin. spp. :—*Surirella ovata* Kütz., *Nitzschia amphibia* Grun., *Rhoicosphenia curvata* Grun., *Fragilaria* spp.

Loc. 31. Scraped from sides of iron drinking trough, near Seaside.

Prin. spp. :—*Cymbella ventricosa* Kütz. (auxospores), *C. cistula* Hemp., *Gomphonema constrictum* Ehb.

Loc. 32. From weir, Powgavie Burn, near Grange.

Prin. spp. :—*Navicula viridula* Kütz., *N. cryptocephala* Kütz.

Loc. 33. From surface of mud in bed of sluggish stream, behind Megginch Castle.

Prin. spp. :—*Cymatopleura solea* W. Sm. *Nitzschia linearis* W. Sm., *Surirella ovata* Kütz., *Navicula cuspidata* Kütz.

Loc. 34. Tough film in rain puddles on road at quarry, Kilspindie. Mixed with Chlorophyceae and Myxophyceae.

Prin. spp. :—*Hantzschia amphioxys* Grun., *Surirella ovata* Kütz. (very small), *Navicula cryptocephala* Kütz.

Loc. 35. From surface of rocks, under waterfall, Kilspindie.

Prin. spp. :—*Navicula viridula* Kütz., *N. cryptocephala* Kütz., *Surirella ovata* Kütz., *Achnanthes coarctata* Breb.

Loc. 36. From ditch, left of road, leading to Rait.

Prin. spp. :—*Hantzschia amphioxys* Grun. and vars., *Surirella ovalis* Breb., *Nitzschia sinuata* Grun., *Achnanthes minutissima* Kütz., *Meridion circulare* Ag.

Contains the interesting *Navicula gibbula* Cl.

Loc. 37. From stones in weir near Longforgan Station.

Prin. spp. :—*Cymatopleura solea* W. Sm., *Navicula rhynchocephala* Kütz., *Nitzschia linearis* W. Sm., *Actinoptychus undulatus* Ehb.

Contains a few brackish forms due to the influx of water from the Tay at very high tides.

Loc. 38. Attached to grass in brackish pools on low road near Invergowrie.

Prin. spp. :—*Amphipleura rutilans* Trent., *Nitzschia navicularis* Grun., *Navicula peregrina* Kütz.

Loc. 39. Carse clay, Invergowrie Road. The clay was obtained from a bank on the north side of the road just below the railway-line, about half a mile west of Kingoodie. This part of the bank had been scooped out and thus exposed the clay. The lower layer of this clay, which is slightly above the level of the public road, is bluish, and contains brackish and marine species in fair abundance. Above this lies a rather yellowish layer, more sandy, and with practically no diatoms. These clays lie unconformably on the Old Red Sandstone. The upper layer probably owes its origin and sandy nature to the reduction of the glacial drift which overlies the sandstone. There is evidence from the species that the water at the time of deposition of the clay was more brackish than it

is in the same locality to-day. Although most of the species found in the clay are common in the river to-day, there are one or two interesting points brought out by a comparison of the lists of recent and fossil forms. Small species are by no means abundant in the clay, and many found in abundance at various localities in recent collections are not represented. Separation of the small species might seem to be readily accounted for by their difference in weight. If this explanation were correct we should expect to find the smaller forms at a higher level, but I have not found this to be so. Also, separation by natural grading could scarcely account for the almost complete removal of all the very small forms from amongst the larger and heavier. Some of the small forms, but by no means all of them, are rather delicate, but I cannot account for their non-appearance by erosion, as the specimens show practically no trace of this. The uncleaned clay contains very little organic matter, the sand is fine and contains a fair percentage of mica. One of the characteristic diatoms in the Tay to-day is *Surirella pyriformis* Kitt., but it does not occur in the Carse clay, and must therefore be considered as a comparatively recent addition to the district. Similar exposures of the clay at Longforgan, Errol, and Glencarse have been examined and have furnished the same species. At these places the clay is part of the 25-foot terrace or raised beach which is considered to mark a pause in the uplift of the land since Glacial times.

Prin. spp. (in order of their abundance) :—*Nitzschia navicularis* Grun., *Paralia sulcata* Kütz., *Hyalodiscus stelliger* Bail., *Actinoptychus undulatus* Ehb., *Rhaponeis amphiceros* Ehb. (and varieties), *Nitzschia bilobata* W. Sm., *Caloneis formosa* Greg.

Forty-eight forms were found in the clay.

Loc. 40. Scraped from submerged wooden piles in quarry pond, Invergowrie. Brackish water.

Prin. spp. :—*Mastogloia elliptica* v. *Dansei* Thw., *Cocconeis pediculus* Ehb., *Synedra pulchella* v. *Smithii* Ralfs., *Rhoicosphenia curvata* Grun.

This is the only locality in the district where an abundance of *Mastogloia* has been found.

Loc. 41. Floating aerated masses in ditch near Invergowrie House.

Prin. spp. :—*Navicula viridula* Kutz. v. *slesvicensis* Grun., *N. cryptocephala* Kütz.

Contains the interesting *N. relicta*, sp. n.

Loc. 42. Olive-green film on porcelain sink, greenhouse, University College, Dundee.

Prin. spp. :—*Achnanthes minutissima* Kütz., *A. minutissima* v. *cryptocephala* Grun., *Navicula minima* Grun.

The collection contains ten species.

Loc. 43. Floating masses from quarry pool, near Linoleum Works, Liff.

Prin. spp. :—*Denticula tenuis* Kütz., *Hantzschia amphioxys* Grun., *Nitzschia* spp.

Contains *Navicula gibbula* Cl.

Loc. 44. Tow-nettings from ponds in North Woods, Camperdown.

Prin. spp. :—*Diatoma tenue* Kütz., *Fragilaria mutabilis* Grun., *F. construens* Grun.

Loc. 45. Washings from mosses and foliose hepatics, Blairfield Quarry, Birkhill. Altitude 450 feet.

Prin. spp. :—*Diatoma hiemale* Heib., *Nitzschia sinuata* Grun., *Diploneis elliptica* Kütz., *Cymbella parva* W. Sm., *C. cymbiformis* Kütz.

Loc. 46. Gelatinous masses on surface of wet rocks, Blairfield Quarry.

Prin. spp. :—*Diatoma hiemale* Heib., *Nitzschia sinuata* Grun., *Diploneis elliptica* Kütz., *Cymbella parva* W. Sm.

Loc. 47. Brownish aerated masses on mosses and foliose hepatics at base of dripping-wet rocks, Blairfield Quarry.

Prin. spp. :—*Cymbella parva* W. Sm., *C. microcephala* Grun., *C. angustata* W. Sm., *Cocconeis flexella* Kütz., *Achnanthes minutissima* Kütz.

This is the only collection in the district in which I have found *Cymbella Cesatii* Rabh.

Loc. 48. Scraped from stones in stream opposite entrance to Balruddery House.

Prin. spp. :—*Diatoma vulgare* Bory, *Gomphonema olivaceum* Lyngb., *Cymbella ventricosa* Kütz., *Surirella ovata* Kütz.

Loc. 49. Gelatinous masses from surface of dripping-wet rocks, Balruddery Quarry.

Prin. spp. :—*Diatoma hiemale* Heib., *Amphora ovalis* Kütz., *Diploneis elliptica* Kütz., *Fragilaria virescens* Ralfs.

Loc. 50. From sides of cement horse trough, and floating aerated masses, Dron Farm.

Prin. spp. :—*Cymbella ventricosa* Kütz. (in auxospore stage), *Navicula radiosa* Kütz., *Synedra* spp., *Nitzschia* spp.

Loc. 51. Brown gelatinous film on stones under fast-flowing water leading into pond, Fowlis.

Prin. spp. :—*Navicula viridula* Kütz., *N. cryptocephala* Kütz., *Cymbella ventricosa* Kütz.

Loc. 52. Floating aerated masses, Piper Dam. The Piper Dam is situated in a circular depression, and receives water from a burn which drains the north side of Blacklaw Hill. A very rich collection was obtained here, containing about 150 distinct forms, including the curious *Mastogloia* ? *canalicula*. Altitude 630 feet.

Prin. spp. :—*Fragilaria capucina* v. *mesolepta* Grun., *Synedra ulna* Ehb., *Cymbella symmetrica*, sp. n.

Loc. 53. Floating aerated masses in dam, Binns Burn, Fowlis Easter. Altitude 600 feet.

Prin. spp. :—*Cymatopleura solea* W. Sm., *Gyrosigma* spp.

Contains *Mastogloia* ? *canalicula*, sp. n.

Loc. 54. Scraped from stones in burn, Littleton Glen. Altitude 500 feet.

Prin. spp. :—*Navicula viridula* Kütz., *Cymbella ventricosa* Kütz. (auxospore stage), *Gomphonema olivaceum* Lyngb.

Loc. 55. Tow-netting from stream leading to Laird's Loch, Tullybaccart, and dark brown filamentous strands attached to plants in stream. Altitude 700 feet.

Prin. spp. :—*Pinnularia major* Kütz., *P. nobilis* Ehb., *P. gentilis* Donk., *P. streptoraphe* Cl., *P. divergens* W. Sm. (auxospores).

One of the most interesting collections in the district contains 110 forms, of which a considerable number are alpine and sub-arctic species.

Loc. 56. Scraped from stones, Lochindores, Tullybaccart. Part of this collection formed a firm skin on stones, the skin being composed of Myxophyceae, mixed with numerous small species of diatoms. Altitude 700 feet.

Prin. spp. :—*Gomphonema constrictum* Ehb., *G.* spp., *Fragilaria* spp., *Navicula radiosa* Kütz., *Cymbella cistula* Hempr.

Loc. 57. Brownish film on soil, surface of road, under slowly trickling water, Tullybaccart. Altitude 700 feet.

Prin. spp. :—*Cymbella ventricosa* Kütz., *C. parva* W. Sm., *Meridion circulare* Ag., *Surirella ovata* Kütz. (small forms), *Navicula viridula* v. *Slesvicensis* Grun.

Loc. 58. Composite collection, Tullybaccart : (*a*) Tow-nettings from pot-holes besides Lochindores ; (*b*) tow-nettings from side of Lochindores ; (*c*) light green flocculence attached to grass in pot-holes, the flocculence consisted of *Zygnema* and *Spirogyra.*

Prin. sp. :—Similar to other collections in the area.

Loc. 59. Light brown very gelatinous covering on stones in stream under road bridge, Tullybaccart. Altitude 700 feet.

Prin. sp. :—*Gomphonema olivaceum* Lyngb. (in auxospore stage).

Loc. 60. From margin of loch near Lundie. Altitude 630 feet.

Prin. sp. :—Similar to those in the Laird's Loch.

Loc. 61. Diatoms associated with filamentous Chlorophyceae in stream, Lundie. Altitude 600 feet.

Prin. sp. :—*Diatoma vulgare* Bory., *Fragilaria mutabilis* Grun.

Loc. 62. Scraped from mill-wheel, Lundie. Altitude 600 feet.

Prin. spp. :—*Nitzschia sinuata* Grun., *Cymbella ventricosa* Kütz. (auxospores), *Gomphonema constrictum* Ehb.

Loc. 63. Floating masses in dam, Castle Farm, Lundie. Altitude 550 feet.

Prin. spp. :—*Cymatopleura solea* W. Sm., *C. elliptica* W. Sm., *Pinnularia major* Kütz., *P. nobilis* Ehb., *P. viridis* Kütz., *Cymbella* spp., *Gyrosigma* spp.

Loc. 64. From marshy ground covered with sphagnum, round the margin of Long Loch. Altitude 720 feet.

Prin. sp. :—Similar to those in Laird's Loch.

Loc. 65. From the margin of Thriepley Loch. Altitude 610 feet.

Prin. sp. :—Similar to those in Laird's Loch.

Loc. 66. Boggy pool, top of Auchterhouse Hill. Altitude 1,200 feet.

Prin. spp. :—*Navicula* spp., *Pinnularia* spp., *Gomphonema* spp., *Melosira* spp. (see loc. 67).

Loc. 67. Pot-hole beside boggy pool, top of Auchterhouse Hill. Altitude 1,200 feet.

Prin. spp. :—*Melosira lineolata* Grun., *M. lyrata* v. *lacustris* Grun., *M. distans* Kütz., *M. crenulata* Kütz.

Contains the curious *Mastogloia* ? *canalicula*.

Loc. 68. From stream, north side of Balluderon Hill. Altitude 1,100 feet.

Prin. spp. :—*Epithemia turgida* v. *granulata* Grun., *E. gibba* Kütz., *Synedra ulna* Ehb., *Eunotia* spp., *Pinnularia* spp.

Loc. 69. Pool beside spring, south side of Craigowl Hill. Altitude 1,100 feet.

Prin. spp. :—*Amphora ovalis* Kütz., *Nitzschia sigmoidea* W. Sm., *Pinnularia nobilis* Ehb., *P. dactylus* Ehb.

Loc. 70. Sphagnum bogs and pools, north side of Craigowl Hill. Altitude 1,300 feet.

Prin. spp. :—*Caloneis alpestris* Grun., *Pinnularia alpina* W. Sm., *P. streptoraphe* Cl., *P. flexuosa* Cl., *Surirella helvetica* Brun., *Cymbella incerta* v. *naviculacea* Grun., *Epithemia gibberula* v. *rupestris* W. Sm., *Melosira nivalis* W. Sm., *Anomoeoneis exilis* Grun.

The collection contained quite a number of alpine and sub-arctic forms.

Loc. 71. From sandy bed of stream at foot of Gallow Hill. Altitude 700 feet.

Prin. sp. :—*Cymbella prostata* Ralfs.

Loc. 72. From water trough, Balkemback, Tealing. Altitude 550 feet.

Prin. sp. :—*Diatoma hiemale* Heib. (almost pure).

Loc. 73. Gelatinous masses scraped from floating logs in Earl Grey Dock, Dundee.

Prin. spp. :—*Navicula crucigera* W. Sm., *N. gracilis* v. *schizonemoides* Grun., *N. ramosissima* f. *amplia* Grun., *N. mollis* W. Sm., *Stauroneis constricta* W. Sm., *Nitzschia* spp.

The collection contains about fifty species.

Loc. 74. From ditch near Templehall, Monikie.

Prin. spp. :—*Navicula viridula* Kütz., *N. cryptocephala* Kütz., *Surirella ovata* Kütz., *Nitzschia palea* W. Sm.

Loc. 75. Rich olive-brown gelatinous covering on stones in Buddon Burn, Templehall, Monikie.

Prin. spp. :—*Gomphonema olivaceum* Lyngb., *Cymbella ventricosa* Kütz., *Achnanthes minutissima* Kütz., *Nitzschia palea* W. Sm., *Navicula cryptocephala* Kütz.

Loc. 76. Delicate brown flocculent matter attached to floating straw in ditch, near Pitairlie Quarry, Monikie.

Prin. spp. :—*Meridion circulare* Ag. (almost pure), *Pinnularia viridis* Kütz., *Surirella ovata* Kütz.

Loc. 77. From stones in Pitairlie Burn, in quarry, near Monikie. The diatoms formed a somewhat tenacious, dark brown film on the stones.

Prin. spp. :—*Navicula viridula* Kütz., *N. cryptocephala* Kütz., *Surirella ovata* Kütz., *Nitzschia palea* W. Sm., *Meridion circulare* Ag.

Loc. 78. Brown flocculent strands attached to submerged stones, and tow-nettings, reservoirs, Monikie.

Prin. spp. :—*Fragilaria crotonensis* Kitt., *F. capucina* Desm., *Diatoma elongatum* Ag., *D. vulgare* v. *Ehrenbergii* Grun., *Asterionella formosa* Hass., *A. formosa* v. *subtilis* Grun., *Meridion circulare* Ag.

Loc. 79. From surface of mud in bed of stream near Carnoustie.

Prin. spp. :—*Cymatopleura solea* W. Sm., *C. elliptica* W. Sm.

Loc. 80. From rocks, pools, and sands at Carnoustie and Easthaven.

Prin. spp. :—*Licmophora* spp., *Pleurosigma* spp., *Coscinodiscus* spp., *Rhabdonema* spp., *Grammatophora* spp., *Biddulphia* spp., *Navicula* spp.

Pleurosigma balticum W. Sm., which is very abundant at Tayport, is very scarce here. Collections from this locality contain almost 200 forms.

Loc. 81. The following is a brief note on the plankton of the Tay Estuary as it has been observed in tow-net collections taken between the east side of the Tay Bridge and the mouth of the river ; from Tayport Harbour ; from off the Bell rock. Most of the collections have been made during the spring and summer, but they are too few and have been taken too irregularly to furnish an adequate record of the plankton of the Estuary. In the tow-nettings the majority of the diatoms observed, 45 species in all, are true marine plankton forms, but a considerable number of bottom-living and littoral species also occur, as well as brackish and freshwater species. There are also a few species such as *Gomphonema geminatum*, dead specimens of which are not infrequent in the collections, which have obviously been carried down the river from the inland districts. The marine plankton diatoms occur in all these collections very sparsely, and no rich developments of neritic species, such as are known to occur every spring and less regularly every autumn around our coasts, have been observed. This may be due to the ebb and flow of the tides in the narrow estuary, the constant rush of water preventing the steady multiplication of the diatoms in any locality. The disturbing action of the water is increased by the large volume of fresh water brought down by the rivers Tay and Earn. The collections often consist largely of mud and sand brought down by these rivers, and mud stirred up by the tidal action, which also accounts for the relative frequency of bottom-living species such as *Actinoptychus undulatus*, *Biddulphia aurita*, *Surirella gemma*, *Pleurosigma* spp., etc., which at times outnumber the true plankton forms in the collection. The samples from Tayport are comparatively clean, possibly because the water there is not subject to tidal action to the same extent. All the marine plankton diatoms are, as is to be expected, species which have been recorded from the North Sea. They are naturally chiefly neritic in character, and the few records we have of oceanic

forms must be looked upon as fortuitous, the specimens having been brought into the estuary from the open water outside. The 45 species recorded constitute a fair proportion of the North Sea plankton diatoms, 85 true plankton forms being the number recorded for the Moray Firth and adjacent waters during recent investigations of that area, carried out by the Fishery Board for Scotland for a period of three to four years.

In the following list the species found in these collections from the estuary are classified according to their mode of occurrence :—

MARINE PLANKTON.	BOTTOM-LIVING ETC., MARINE.	FRESHWATER AND BRACKISH.
Asterionella japonica.	Actinoptychus undulatus.	Amphiprora spp.
Biddulphia mobiliensis.	Berkleya sp. (Amphipleura).	Amphora spp.
Cerataulina Bergonii.	Biddulphia aurita.	Asterionella fromosa.
*Chaetoceros boreale.	B. granulata.	Cymbella spp.
C. constrictum.	Cocconeis sp.	Diatoma elongatum.
C. curvisetum.	Grammatophora serpentina.	Fragilaria sp.
C. danicum.	Licmophora spp.	Gomphonema geminatum.
C. debile.	Melosira Borreri.	Melosira spp.
*C. decipiens.	Nitzschia closterium.	Meridion circulare.
*C. densum.	Pleurosigma affine.	Navicula spp.
C. diadema (and with spores).	P. angulatum.	Pinnularia spp.
C. laciniosum (and with spores).	P. balticum.	Synedra spp.
	P. fasciola.	Tabellaria fenestrata.
C. scolopendra.	P. quadratum.	T. fen. v. asterion.
C. simile.	P. spp.	T. flocculosa.
C. skeleton.	Rhabdonema adriaticum.	
C. subtile.	Rhaphoneis amphiceros.	
C. teres (and with spores).	Navicula crucigera.	
Coscinodiscus concinnus.	N. (Schizonema) spp.	
*C. excentricus.	Surirella gemma.	
C. lineatus.	S. pyriformis.	
*C. marginatus.	S. splendida.	
*C. radiatus.		
*C. subbuliens.		
Coscinosira polychorda.		
Ditylium Brightwellii.		
Guinardia flaccida.		
Hyalodiscus stelliger.		
Lauderia borealis.		
Leptocylindricus danicus.		
Nitzschia delicatissima.		
N. seriata.		
Paralia sulcata.	MARINE PLANKTON (con.).	
Rhizosolenia delicatula.	Skeletonema costatum.	
R. faeroensis.	Stephanopyxis turris.	
*R. semispina.	Streptotheca thamensis.	
R. setigera.	Thalassiosira gravida.	
R. Shrubsolei.	T. decipiens.	
*R. styliformis.	T. Nordenskioldii.	
R. Stolterfothii.	Thalassiothrix nitzschioides.	

* Oceanic species (remainder neritic).

Note on the classification used in this paper.—The classification given at the end of Peragallo's 'Diatomées Marines de France' (texte) has been used, except where otherwise stated.

Order 1. PENNATAE.

Tribe 1. DIATOMEAE HETEROIDAE.

Family I. ACHNANTHEAE*.

RHOICOSPHENIA Grun.

R. CURVATA Kütz. ; V. H. Syn. xxvi, 1–3. Loc. 11, 20, 21, 23, 24, 37, 40, 43, 48, 51, 54. Fairly abundant. Frequently occurs as an epiphyte on *Cladophora*.

R. CURVATA v. MARINUM V. H. ; V. H. Syn. xxvi, 4. Loc. 8, 38, 80. Not abundant.

R. VAN-HEURCKII Grun. ; V. H. Syn. xxvi, 5–9. Loc. 25. Rare.

ANORTHONEIS Grun.

A. EXCENTRICA Donk. ; T. M. S. vi, pl. iii, f. 11. Loc. 8, 10. Rare.

COCCONEIS (Ehb.) Cl.

C. GRANULIFERA Grev. ; S. N. D. pt. ii, pl. ii, f. 36–7. Loc. 8, 27, 80. Rare.

C. PEDICULUS Ehb. ; V. H. Syn. xxx, 28, 30. (Text-fig. 1.) Loc. 7, 8, 23, 26, 27, 40, 48, 53, 59, 62, 63, 75, 78. This and the following species are general and frequently abundant in fresh water. Both occur as epiphytes on non-slimy green algae, e.g. *Vaucheria*, *Cladophora*, and *Rhizoclonium*, and on angiospermous hydrophytes. From Morton Lochs, Tentsmuir, a fine collection of this species was found growing as an epiphyte on *Rhizoclonium hieroglyphicum*. The average size of the species was $24\,\mu \times 16\,\mu$. The frustule consists of four distinct parts :—Upper valve, girdle, loculiferous annulus, and lower valve. The girdle is attached to the upper valve and overlaps the rim of the loculiferous annulus which lies inside the lower valve, and is closely applied to it. The loculiferous annulus bears from six to twelve rudimentary marginal loculi the walls of which are reduced to fine bars scarcely raised above the lower valve. These loculi have neither upper nor lower partitions. The stout hyaline annulus from which the delicate ribs project lies over a structureless

* In this family Cleve's classification has been followed.—S. N. D..

peripheral area of the lower valve. The lower valve has a very short rim, and the rim of the annulus to which it is closely attached extends beyond it.

C. PLACENTULA Ehb. ; V. H. Syn. xxx, 26, 27. Loc. 32, 53, 56. Fairly abundant.

C. PLACENTULA v. LINEATA Ehb. ; V. H. Syn. xxx, 31, 32. Loc. 13, 23, 27, 40, 49, 51, 53, 54, 66, 78. General and fairly abundant.

C. PLACENTULA v. EUGLYPTA Ehb. ; V. H. Syn. xxx, 33, 34. Loc. 7, 65, 68. Not so general as the above.

C. SCUTELLUM Ehb. ; V. H. Syn. xxix, 1-3. Loc. 8, 26. Fairly abundant.

C. SCUTELLUM v. MINUTISSIMA Grun. ; V. H. Syn. xxix, 12. Loc. 22, 28. Not abundant.

C. SCUTELLUM v. PARVA Grun. ; V. H. Syn. xxix, 8, 9. Loc. 35. Not abundant.

C. SCUTELLUM v. STAURONEIFORMIS W. Sm. ; V. H. Syn. xxix, 10, 11. Loc. 8, 12, 22, 80. Fairly abundant.

C. SCUTELLUM v. ORNATA Grun. ; V. H. Syn. xxix, 6, 7. Loc. 80. Rare.

C. SCUTELLUM v. DISTANS (Greg.) A. S. ; A. S. Atl. cxciii, 29, 36, 40. Loc. 8, 26. Rare.

EUCOCCONEIS Cl.

E. DIRUPTA Greg. v. TYPICA Cl. ; V. H. Syn. xxix, 13-15. Loc. 8, 80. Somewhat rare.

E. FLEXELLA Kütz. ; V. H. Syn. xxvi, 29-31. Loc. 6, 14, 36, 46, 47, 49, 52, 59, 64, 69, 70. A fairly common sub-alpine form.

MICRONEIS Cl.

ACHNANTHES (MICRONEIS) MINUTISSIMA Kütz. ; V. H. Syn. xxvii, 35-38. Loc. 2, 4, 7, 16, 19, 20, 21, 24, 25, 28, 31, 32, 35, 36, 41, 43, 45, 46, 47, 48, 49, 59, 61, 62, 63, 64, 65, 70, 72, 75, 78. Ubiquitous in fresh water, and probably the commonest of all freshwater diatoms. Frequently occurs unmixed with other species.

A. MINUTISSIMA Kütz. v. CRYPTOCEPHALA Grun. ; V. H. Syn. xxvii, 20-23. Loc. 3, 19, 66. Fairly abundant.

A. EXILIS Kütz. ; V. H. Syn. xxvii, 16-19. Loc. 41. Rare. The three small freshwater species, *A. exilis, linearis,* and *microcephala,* all occur as stalked epiphytes on filamentous algae such as *Cladophora* and *Rhizoclonium.*

A. LINEARIS W. Sm. ; V. H. Syn. xxvii, 31, 32. Loc. 21. Not abundant.

A. LINEARIS v. PUSILLA Grun. ; V. H. Syn. xxvii, 33, 34. Loc. 14, 70. Not abundant.

A. MICROCEPHALA Kütz. ; V. H. Syn. xxvii, 20–23. Loc. 6, 36, 43, 50. Fairly abundant.

A. BIASOLETTIANA Kütz. ; V. H. Syn. xxvii, 27, 28. Loc. 30, 72. Somewhat rare.

A. DELICATULA Kütz. ; V. H. Syn. xxvii, 3, 4. Loc. 21, 26, 28, 40, 73. A brackish species.

A. SIMILIS, sp. n. (Text-fig. 2.) Valve elliptic-lanceolate with produced sub-acute ends. L. 20–30 μ, b. 7–10 μ. Upper valve with narrow lanceolate area, striae 14 *, parallel at the middle and radiate towards the ends. Lower valve with indistinct axial area and large central orbicular area, striae 14, radiate throughout. Loc. 8. Fairly abundant. [See Appendix, p. 304.]

A. HAUCKIANA Grun. ; V. H. Syn. xxvii, 14, 15. Loc. 8, 26, 27. Not abundant. The following measurements were obtained from specimens in Loc. 27 :—13 $\mu \times 6\ \mu$. S. 13 (upper), 12 (lower).

A. AFFINIS Grun. ; V. H. Syn. xxvii, 39, 40. Loc. 2, 68. Rare.

* i.e. 14 in 10 μ.

EXPLANATION OF TEXT-FIGS. 1 to 20 (p. 235).

Magnification × 1,000, except figs. 1, 9 a.

1. *Cocconeis Pediculus* Ehb. 1, upper valve ; 2, girdle ; 3, lower valve ; 4, annulus ; 5, section of upper valve ; 6, section of girdle ; 7, section of lower valve ; 8, section of annulus ; 9, union of upper valve and girdle ; 10, union of lower valve and annulus ; 11, section of frustule : p. 232.
2. *Achnanthes similis*, sp. n. a, lower valve ; b, upper valve : p. 234.
3. *Mastogloia canalicula*, sp. n. a, valve ; b, girdle view ; c, side view of valve : p. 238.
4. *Caloneis sublinearis*, sp. n. : p. 240.
5. *Neidium capitatum*, sp. n. : p. 242.
6. *Neidium Iridis* Ehb. v. *bryophilum*, v. nov. : p. 242.
7. *Neidium Iridis* Ehb. v. *robusta*, v. nov. : p. 242.
9. *Diploneis nitescens* Greg. v. *candida*, v. nov.   9 a. Centre of valve, × 2,000 : p. 244.
10. *Navicula mutica* Kütz. f. *gibbosa* : p. 245.
11. *Navicula mutica* Kütz. f. *ornata* : p. 245.
12. *Navicula mutica* v. *pulchra*, v. nov. : p. 245.
13. *Navicula inflata* Donk. v. *rostrata*, v. nov. : p. 246.
14. *Navicula gibbula* Cl. : p. 248.
15. *Navicula relicta*, sp. n. b, girdle view : p. 248.
16. *Stauroneis parvula* Grun. v. *attenuata*, v. nov. : p. 249.
17. *Navicula peregrina* Ehb. v. *producta*, v. nov. : p. 252.
18. *Navicula distans* W. Sm. : p. 254.
19. *Navicula serpentina*, sp. n. : p. 255.
20. *Anomoeoneis sphaerophora* v. *intermedia*, v. nov. : p. 256.
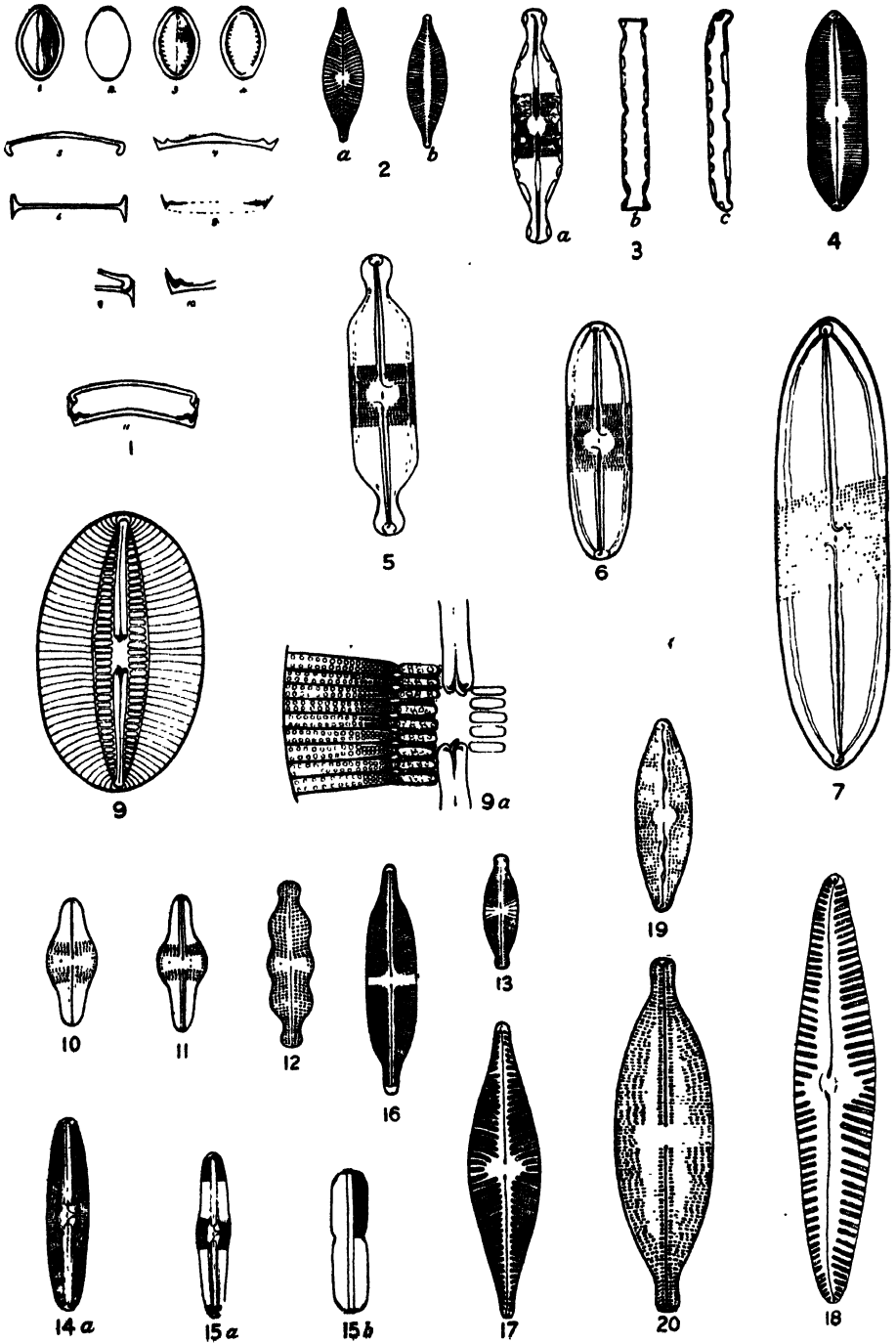
ACHNANTHIDIUM (Kütz.) Heib.

A. (ACHNANTHIDIUM) LANCEOLATA Breb.; V. H. Syn. xxvii, 8–11. Loc. 1, 6, 7, 11, 12, 20, 25, 26, 30, 33, 34, 35, 41, 47, 48, 53, 54, 57, 61, 62, 64, 67, 70, 71, 73. General in fresh water and frequently abundant.

A. LANCEOLATA Breb. v. DUBIA Grun.; V. H. xxvii, 12, 13. Loc. 6, 19, 32, 68, 72. It is worthy of note that this variety is seldom found with the type in this district.

A. COARCTATA Breb.; V. H. Syn. xxvi, 17–20. Loc. 35, 36, 38. This freshwater species is abundant in Loc. 35 (rocks under waterfall, Kilspindie).

A. BREVIPES Ag. v. TYPICA Cl.; V. H. Syn. xxvi, 10–12. Loc. 8, 18. Not abundant.

A. BREVIPES v. PARVULA Kütz.; V. H. Syn. xxvi, 25–28. Loc. 8, 22. Not abundant.

A. BREVIPES v. INTERMEDIA Kütz.; V. H. Syn. xxvi, 21–24. Loc. 8, 27, 73. Not abundant.

ACHNANTHES Bory.

A. LONGIPES Ag.; V. H. Syn. xxvi, 13–16. Loc. 8. Not abundant.

EXPLANATION OF TEXT-FIGS. 21 a to 38 (p. 237).

Magnification 1,000, except 30.

21 a. *Pinnularia divergens* W. Sm.   Post-auxospore form: p. 259.
22. *P. divergentissima* Grun. f. *subacuta*: p. 259.
23. *P. bacilla*, sp. n.: p. 259.
24. *P. Westii*, sp. n.: p. 261.
25. *Gyrosigma distortum* W. Sm. v. *undulata*, v. nov.: p. 267.
26. *Amphiprora lata* Grev. v. *angustior*, v. nov.: p. 268.
27. *A. robusta*, sp. n.: p. 269.
28. *Cymbella delicatula* Kütz. v. *intermedia*, v. nov.: p. 269.
29. *C. symmetrica*, sp. n.: p. 270.
30. *C. cistula* Hempr.   a, cyst: p. 271.
31. *Amphora ovalis* Kütz.   Sporangial form: p. 272.
32. *Nitzschia Tryblionella* Hantz. v. *recta*, v. nov.: p. 280.
33. *N. sinuata* Grun.   b, post-auxospore form: p. 281.
34. *Hantzschia amphioxys* Grun. v. *lanceolata*, v. nov.: p. 286.
35. *H. rigida*, sp. n.: p. 286.
36. *Fragilaria brevistriata* Grun. v. *turgida*, v. nov: p. 292.
38. *Cyclotella Meneghiniana* Kütz. v. *stigmata*, v. nov.: p. 299.
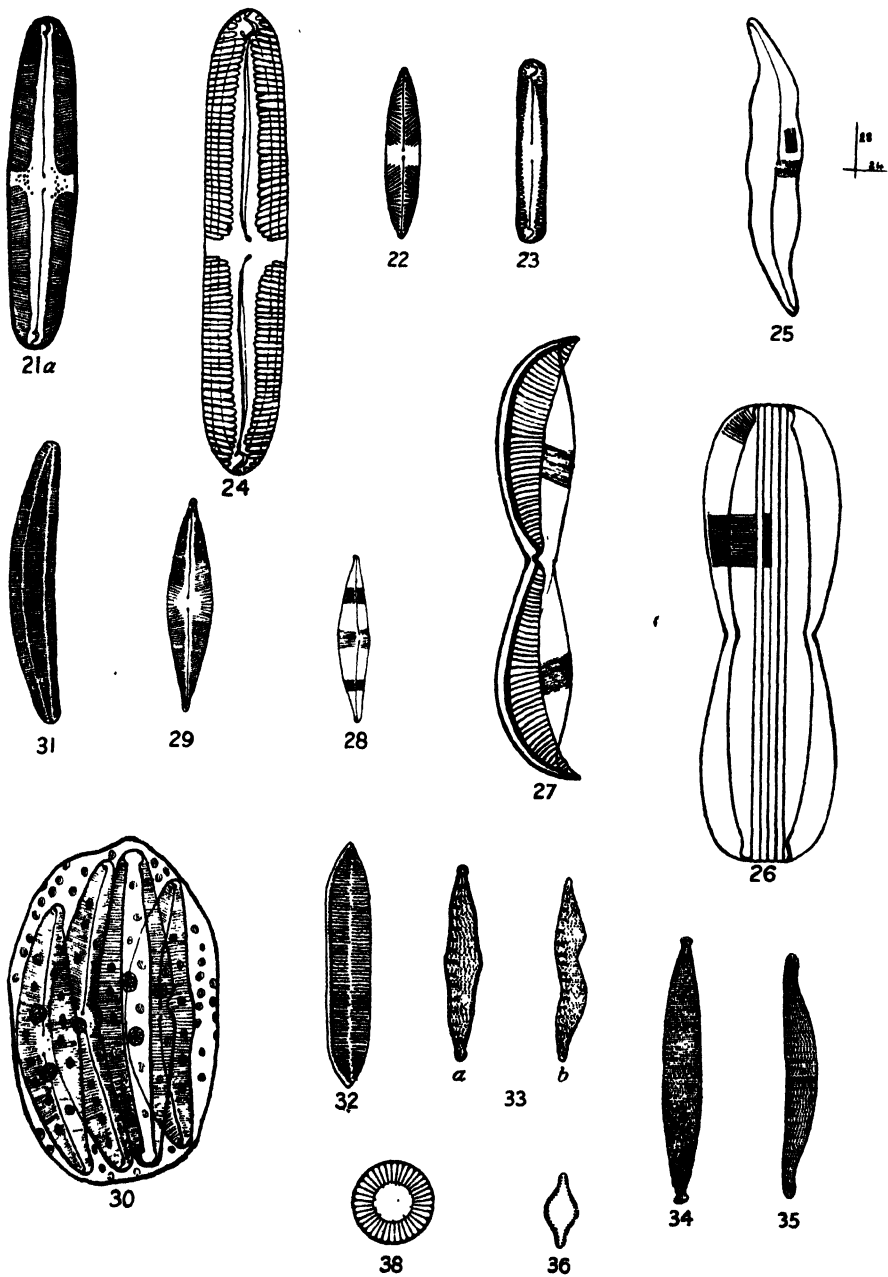
Tribe 2. DIATOMEAE NAVICULOIDAE.

Family II. MASTOGLOIEAE.

MASTOGLOIA Thw.

M. GREVILLEI W. Sm. ; B. D. lxii, 389.   Loc. 70, 71.   Rare.

M. ELLIPTICA Ag. ; V. H. Syn. iv, 19.   Loc. 40.   Fairly abundant.

M. ELLIPTICA v. DANSEI Thw. ; V. H. Syn. iv, 18.   Loc. 40.   Very abundant.

(M. ?) CANALICULA, sp. n.   (Text-fig. 3.)   Valve linear to linear-lanceolate, with broad capitate ends.   Frustule in girdle view narrow, linear with parallel margins, slightly constricted at the middle and at the ends.   Small, roundish, marginal loculi (?), about 3 in 10 μ.   In the middle of each half of the raphe a loculus or canal.   Striae parallel, about 28 in 10 μ.   Axial area very narrow, central area roundish, small.   L. 40–45 μ, b. 8–9 μ.   Loc. 52, 53, 57.   Rare. This curious diatom has the loculi in the raphe similar to those in *Rouxia* Per. & Herib. (Diat. d'Auv. i, 12).   I place this species here provisionally. [See Appendix, p. 304.]

Family III. NAVICULEAE.*

CALONEIS Cl.

C. BACILLARIS Greg. ; M. J. iv, pl. i, fig. 24.   Loc. 14, 19.   Rare.

C. BACILLUM (Grun.) Mer. ; V. H. Syn. xii, 28, 31, 33.   Loc. 14, 52, 70. Occurs frequently in peaty bogs.

C. FASCIATA Lagerst. ; V. H. Syn. xii, 34.   Loc. 2, 14, 16, 19, 41, 52, 53, 59. Commonly found in peaty bogs, and frequently associated with *Hypnum* etc. Under this species Cleve includes a number of forms—*N. fonticola* Grun., *N. fontinalis* Grun., *N. lacunarum* Grun., and *Stauroneis (Caloneis) bacillum* Grun.   Cleve has here carried the condensation of species too far, as the last species is hardly to be reduced to a form of *C. fasciata*, and should be considered as a separate species.   Indeed, in many specimens of *C. fasciata*, the longitudinal lines are not visible, and this species bears such a strong resemblance to members of the group *Parallelistriata*, of the genus *Pinnularia*, that both Grunow and Mereschkowsky have considered it to be a *Pinnularia*.   Hustedt (' Die Bacillariaceen-Vegetation des Sarekgebirges', p. 553), although inclined to agree with Mereschkowsky, leaves the matter for further investigation.

C. SILICULA Ehb. v. ALPINA Cl. ; V. H. Syn. xii, 21.   Loc. 14, 52, 55, 64, 70. This northern form, which is quite general along the Sidlaws, also occurs in Forgan Bog, Fifeshire.

C. SILICULA v. GIBBERULA Kütz. ; V. H. Syn. xii, 19.   Loc. 14, 33, 52. Occurs in similar localities to the above, but is not so common.

* Cleve's classification, as in S. N. D.

C. SILICULA v. GENUINA Cl. ; V. H. Syn. xii, 18. Loc. 7, 13, 14, 23, 33, 52, 55, 60, 69, 70. More widespread than the other varieties, but never very abundant.

C. SILICULA v. VENTRICOSA Donk. ; V. H. Syn. xii, 24. Loc. 6, 14, 52, 55, 63. Not abundant.

C. SILICULA v. CUNEATA Herib. ; Diat. Foss, d'Auv. ix, 29. Loc. 14, 38. Rare. Not included by Cleve in S. N. D. L. 40 μ, b. 8 μ. S. 20.

14 b

21 b   8   37
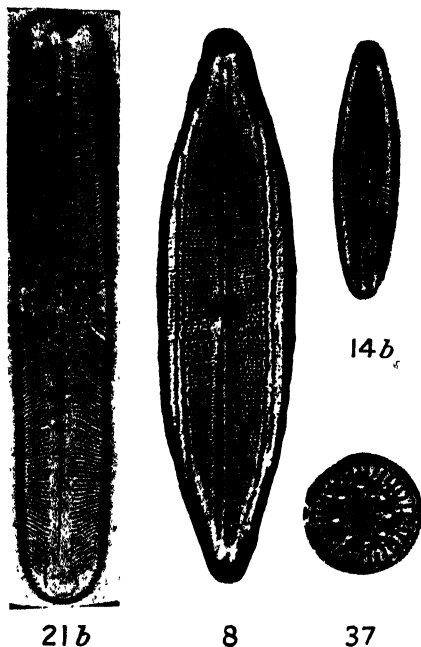
Magnification × 1.000.

8. *Neidium amphigomphus* Ehb. v. *intermedium*, v. nov. : p. 242.
14 b. *Navicula gibbula* Cl. photo : p. 248.
21 b. *Pinnularia divergens* W. Sm. Post-auxospore form : p. 259.
37. *Cyclotella sexnotata* Behy. Form with eight puncta : p. 299.

C. SILICULA v. JENISSEYENSIS Grun. f. PARVA, f. nov. Differs from the variety in its smaller size. L. 25-30 μ, b. 7-8 μ. S. circa 20. Loc. 6. Not abundant. [See Appendix, p. 304.]

C. ALPESTRIS Grun. ; V. H. Syn. xii, 30. Loc. 45, 49, 70. Not abundant.
Average size in Loc. 49 :—l. 57 μ, b. 10 μ. S. 20. And in Loc. 70 :—l. 62 μ, b. 10 μ. S. 20.
A typical northern or alpine form which at Lake Marlaren, Sweden, occurs in the post-glacial mud. It is interesting to compare the three localities in the district in which this species is found ;—Loc. 45 in washings from *Sphagnum*,

Blairfield Quarry, Birkhill; Loc. 49, from surface of dripping rocks, quarry, Balruddery Den; Loc. 70, *Sphagnum* bogs and pools north side of Craigowl, Sidlaws.

CALONEIS OBTUSA W. Sm.; Donk. B. D. iii, 12; A. S. Atl. 263, f. 11.   Loc. 52, 55, 58.   Not common.

A northern or sub-arctic form which in this district is confined to the Sidlaws. Most abundant in the *Hypum* and *Sphagnum* bogs.   The sub-marginal lines in this species are caused by internal chambers or loculi such as are found in the genus *Pinnularia*.   These loculi can be seen if the valve is mounted on its edge.   According to Heiden (A. S. Atl., l.c.) this species is removed from the genus *Caloneis* and is given its former name of *N. hebes* Ralfs, on account of the absence of the characteristic longitudinal lines.   The valve is very convex near the margins, and the loculi or chambers lie on this convex part.   These chambers at a certain focus cause the faint longitudinal lines.   Although the structure indicates that it is a *Pinnularia*, for the present it is retained here.

C. LIBER W. Sm. v. GENUINA Cl.; V. H. Syn. xii, 36.   Loc. 8, 80.   Not common.

C. FORMOSA Greg.; T. M. S. vi, pl. v, fig. 6.   Loc. 8, 39.   One of the most abundant fossil forms in the blue clay of the Carse of Gowrie, at Longforgan, Invergowrie, Errol, and Glencarse.

C. FORMOSA v. HOLMIENSIS Cl.; Cl. N. R. D. ii, 18.   Loc. 8, 39.   As abundant as the type.

C. AMPHISBOENA Bory; V. H. Syn. xi, 7.   Loc. 7, 14, 19, 23, 26, 27, 52, 53, 60, 63, 71.   General in fresh water and frequently abundant.

C. AMPHISBOENA v. SUBSALINA Donk.; B. D. iv, 2.   Loc. 8, 9, 26, 27, 28, 29, 38.   Common in brackish water; the most abundant of the three varieties in Loc. 27.

C. AMPHISBOENA v. LIBURNICA Grun.; V. H. Syn. xi, 3.   Loc. 27.   Not abundant.

C. AMPHISBOENA v. FENZLII Grun.; V. H. Syn. xi, 5.   Loc. 27.   The least abundant of the three varieties in this locality.   In the Port Allen collection there occur besides the type and the three varieties a number of intermediate or transition forms, the whole giving a very good example of progressive variation in a species.   This agrees with Cleve's statement on the varieties of this species—' All these species are closely connected, so that it seems to me impossible to regard them as distinct species.'

C. BREVIS Grev.; Diat. of the Clyde, ix, 4.   Loc. 8.   Rare.

C. SUBLINEARIS, sp. n.   (Text-fig. 4.)   Loc. 63.   Not abundant.   Valve broadly linear with sub-cuneate ends.   Axial area gradually widening towards the

centre where it suddenly dilates to form an orbicular area. Raphe straight with hook-shaped terminal fissures and small, somewhat distant central pores. Striae parallel, slightly radiate at the ends, finely granular but not distinctly punctate. Longitudinal lines infra-marginal. L. 30–40 μ, b. 10–13 μ. S. 16. This species bears a certain resemblance to *C. brevis*, a salt-water form. [See Appendix, p. 304.]

C. LATIUSCULA Kütz.; V. H. Syn. Suppl. pl. B. 29. Loc. 70. Rare. This is the largest freshwater species of the genus that occurs in the district. It is usually found in the larger lakes in Scotland, Sweden, and Switzerland, and may be considered a sub-alpine form. Found on the north side of Craigowl in *Sphagnum* pools and bogs.

NEIDIUM Pfitzer.

The representatives of this genus occurring in the district are most commonly met with in boggy pools and marshy ground, especially on the higher levels of the Sidlaws.

There is great variation in the size and form of the species, so much so that the whole genus represents a series of very closely connected forms, making it a matter of difficulty to clearly define the species.

The collection from Loc. 64 (Long Loch, Sidlaws) contains a number of interesting forms, one of which (*N. capitatum*) I consider to be a new species, and three of which are named as new varieties (*N. Iridis* v. *bryophilum*, occurring chiefly in boggy pools; *N. Iridis* v. *robusta*; *N. amphigomphus* v. *intermedium*). With the addition of these new forms the series is practically complete.

N. BISULCATUM Lagerst.; Spitz. D. i, 8. A. S. Atl. xlix, 15, 17. Loc. 55, 69. Rare. An alpine species which in this district is confined to the Sidlaws.

N. AFFINE Ehb. v. UNDULATA Grun.; V. H. Syn. xiii, 6. Loc. 66. Rare. A sub-alpine form only found in this district in the boggy pool at the top of Auchterhouse Hill. Related to *N. bisulcatum*. S. 24–26.

N. AFFINE V. AMPHIRHYNCHUS Ehb. f. MINOR; S. N. D. part i, 68. Loc. 2, 6, 7, 14, 19, 26, 52, 59, 63, 64, 65. Quite general in boggy pools, but never abundant.

N. AFFINE V. AMPHIRHYNCHUS f. MAJOR; Donk. B. D. v. 9. Loc. 6, 52. Not common. Average size in Loc. 6 :—l. 95 μ, b. 11 μ. S. 16.

N. AFFINE V. GENUINA Cl. f. MINOR; A. S. Atl. xlix, 20–23. Loc. 5, 6, 7, 14, 55. Not very abundant. This form links up with the v. *amphirhynchus*. In some specimens the raphe at the centre makes a somewhat sharp right-angled bend and extends to the striae. Measured specimens :—40 $\mu \times$ 10 μ; S. 22. 69 $\mu \times$ 14 μ; S. 20. 52 $\mu \times$ 14 μ; S. 20.

N. AFFINE V. GENUINA Cl. f. MEDIA; M. J. 1854, ii, 8. Loc. 5, 13, 14, 52, 53, 55, 58, 63, 65. Much more general than f. *minor*. An average specimen measured :—72 $\mu \times$ 16 μ. S. 16.

N. PRODUCTUM W. Sm. ; B. D. xvii, 144. Loc. 33, 69. Somewhat rare.

N. CAPITATUM, sp. n. (Text-fig. 5.) Loc. 64. Somewhat rare. Valve linear with capitate ends. L. 50–60 μ, b. 12–15 μ. S. 20. Striae delicate. Related to *N. productum*, from which it differs in size, parallel sides, and finer striation. [See Appendix, p. 304.]

N. IRIDIS Ehb. ; A. S. Atl. xlix, 2. Loc. 2, 14, 52, 64, 71. All the specimens of this species found in the district have been of rather small size.

N. IRIDIS v. MINOR O. Müller ; A. S. Atl. xlix, 3. Loc. 14, 64. Not abundant.

N. IRIDIS v. BRYOPHILUM, v. nov. (Text-fig. 6.) Loc. 5, 6, 13, 14. Not uncommon. Valve linear, with almost parallel margins, narrowed towards the rounded ends. L. 40–50 μ, b. 13–17 μ. S. 17–18. Puncta 17. This form resembles the diatom figured in A. S. Atl. xlix, 7, but differs in being longer and narrower. Schmidt says of this ' vielleicht *N. dubia* (E. ?) Greg.' The text-figure, however, represents a diatom quite distinct from *N. dubium*, which occurs with the above in the Forgan Bog collection. This new variety, which is not uncommon in the district, is distinct from the v. *minor* O. Müll. (' Hochseen der Riesengebirges ', p. 17), although he mentions that forms intermediate with *N. bisulcatum* occur. The v. *bryophilum* also resembles *N. bisulcatum* in form. L. 40–70 μ, b. 13–17 μ. S. 18. Puncta 18. [See Appendix, p. 304.]

N. IRIDIS v. ROBUSTA, v. nov. (Text-fig. 7.) Loc. 64. Somewhat rare. Valve linear-elliptical with somewhat cuneate ends. L. 90–100 μ, b. 23–26 μ. S. 12 oblique, robust. Puncta 12. [See Appendix, p. 304.]

N. AMPHIGOMPHUS Ehb. ; V. H. Syn. xiii, 2. Loc. 56, 71. Somewhat rare.

N. AMPHIGOMPHUS v. INTERMEDIUM, v. nov. (Text-fig. 8.) Loc. 64. Not common. Valve broadly linear with sub-cuneate ends. L. 80–95 μ, b. 20–25 μ. S. 15. Puncta 16. Connects *N. amphigomphus* with *N. affine* v. *amphirhynchus* f. *major*. [See Appendix, p. 304.]

N. DUBIUM Ehb. ; V. H. Syn. Suppl. pl. B. 32. Loc. 6, 14, 68, 70. Fairly general in peaty bogs.

DIPLONEIS Ehb.

DIPLONEIS HYALINA Donk. ; A. S. Atl. lxx, 1–5. Loc. 8, 9, 26, 27, 80. Not uncommon from Carnoustie up to Glencarse.

D. SUBORBICULARIS Greg. ; A. S. Atl. viii, 2, 3, 5. Loc. 8, 39. Rare.

D. INCURVATA Greg. ; T. M. S. iv, pl. v, 13. Loc. 10. Somewhat rare.

D. INTERRUPTA Kütz. ; A. S. Atl. xii, 3, 4, 5, 11. Loc. 8, 26, 39. Not abundant. The costae are interrupted at the middle of the valve outside the sulcus.

D. BOMBOIDES A. S. ; A. S. Atl. xiii, 36. Loc. 39. Rare.

D. DIDYMA Ehb. ; V. H. Syn. ix, 5, 6, Suppl. pl. B. 20. Loc. 8, 27, 39. Not common.

D. BOMBUS Ehb. ; Diat. of the Clyde, ix, 12. Loc. 8. Rare.

D. BOMBUS v. EGENA A. S. ; A. S. Atl. xiii, 10. Loc. 26, 27, 30, 39. Not uncommon. This variety has three longitudinal lines on either side of the raphe.

D. APIS Ehb. ; Donk. B. D. viii, 3. M. D. de Fr. xix, 3–8. Loc. 8, 39, 80. Not uncommon.

Under *D. chersonensis* Grun., Cleve remarks : ' This very widely distributed species is usually regarded as *N. apis* Ehb. I am unable to make out what this name, as is the case with so many others of the names given by Ehb., may denote. *N. apis* of Donkin (B. D. viii, 3) and of Schmidt (Atl. xii, 16 ; lxix, 41, 43, 44) are unknown to me. Specimens from England in the collection of Grove are identical with *D. incurvata*.' Peragallo (M. D. de Fr. 122) says : ' Je ne puis, avec Cleve, réunir cette espèce à côtes fines avec le *N. chersonensis* dont l'aspect est tout autre, bien que la striation soit semblable.' The specimens from Tayport and Carnoustie, and also those from the blue clay of the Carse of Gowrie agree with Donkin's figure, which, however, does not show the structure of the valve very clearly. Peragallo's figures are very good.

D. ELLIPTICA Kütz. ; A. S. Atl. vii, 29, 32. Loc. 6, 7, 14, 23, 29, 45, 46, 49, 51, 52, 55, 58, 59, 63, 64, 65, 68, 69, 70, 79. The commonest species of the genus found in the district, occurring in 30 per cent. of the freshwater collections. Somewhat variable in size and striation.

D. PUELLA Cl. ; V. H. Syn. x, 11. Loc. 8, 16. Rare. According to Cleve, this species differs only in its small size and indistinct alveoli from *D. elliptica*, with which it is connected by intermediates. In Loc. 16 it is unaccompanied by the typical *D. elliptica*.

D. OCULATA Breb.; V. H. Syn. ix, 19. Loc. 72. Rare. Not previously recorded in Britain.

D. OVALIS Hilse ; Diat. of Fin. pl. ii, 3. Loc. 8, 13, 14, 29, 52, 55, 59, 64, 66, 68, 69. Not so general as *D. elliptica* and never so abundant, and can be distinguished from that species by its larger, rounded, central nodule. Cleve gives the maximum size as $43 \mu \times 26 \mu$. This is greatly exceeded by specimens from Forgan Bog, one measuring $58 \mu \times 23 \mu$. Costae 13 ; puncta 13.

D. OVALIS v. OBLONGELLA Naegeli ; V. H. Syn. x, 12. Loc. 6, 15, 19, 46, 47, 52, 54, 55, 58, 64. Widely distributed, but never abundant.

D. OVALIS v. OBLONGELLA f. GIBBOSA, f. nov. Differs from the variety in being slightly gibbous at the centre. Loc. 14. [See Appendix, p. 305.]

D. FUSCA Greg. v. SUBRECTANGULARIS Cl. ; A. S. Atl. vii, 4. Loc. 26. Very rare.

D. LITTORALIS Donk. ; B. D. i, 2. Loc. 8, 80. Somewhat rare in both localities.

DIPLONEIS VACILLANS A. S., f. B. ; A. S. Atl. viii, 34–36. Loc. 80. Rare.

D. SMITHII Breb. ; A. S. Atl. vii, 16, 17. Loc. 8, 27, 39, 80. Not abundant. The maximum size given by Cleve is 59 $\mu \times$ 35 μ. In localities 8 and 80 specimens measuring up to 68 μ are found. There is considerable variation in the robustness of the markings in this species. In some specimens the alveoli are made out only with difficulty, whilst in others they are robust and easily seen as in *D. major* Cl.

D. NITESCENS Greg. v. CANDIDA, v. nov. (Text-figs. 9, 9 a.) Loc. 80. Not abundant. Valve elliptical, slightly sub-rectangular. L. 50–60 μ, b. 28–32 μ. Central nodule small, rectangular ; horns very narrow, indistinct. Furrows wide, their outer margins enclosing a lanceolate space one-third as broad as the valve, crossed by costae which alternate with double rows of imperfect alveoli. Costae 8 in 10 μ, alternating with double rows of alveoli, which become more widely separated and distinct nearer the margins, 14–16 in 10 μ. [See Appendix, p. 305.]

D. CRABRO Ehb. v. PANDURA Breb. ; V. H. Syn. ix, 1. Loc. 10. Rare.

D. CRABRO v. MULTICOSTATA Grun. ; V. H. Syn. ix, 2. Loc. 80. Not abundant.

NAVICULA Bory.

In the sub-division of this large genus I have followed, in general, the classification of Cleve (S. N. D.).

Section Orthostichae Cl.

NAVICULA GREGARIA Donk. ; V. H. Syn. viii, 12–15. Loc. 8. Fairly abundant.

N. HALOPHILA Grun. ; V. H. Syn. Suppl. pl. B. 30. Loc. 9. Rare.

N. CUSPIDATA Kütz. ; V. H. Syn. xii, 4. Loc. 6, 7, 8, 14, 23, 26, 27, 33, 43, 52, 53, 56, 60, 63, 69, 71. General in fresh water and in peaty bogs, but never very abundant. The typical form of this species (that is, the form with acute ends) does not occur in the district, the common local form having somewhat produced sub-acute ends.

N. CUSPIDATA v. AMBIGUA Ehb. ; V. H. Syn. xii, 5. Loc. 3, 7, 24, 53, 71. Not so general as the type.

N. CUSPIDATA v. HERIBAUDII Per. ; Diat. d'Auv. iv, 6. Loc. 6. Rare. Perhaps only a post-auxospore form of *C. cuspidata*. L. 130 μ, b. 30 μ. S. 10 (12 at the ends), slightly radiate, finely punctate, puncta 22 in 10 μ.

N. SPICULA Dickie ; V. H. Syn. iv, 9. Loc. 8. Rare.

N. CRUCIGERA W. Sm. ; V. H. Syn. xvi, 1. Loc. 8, 73. Very abundant in Earl Grey Dock, where it formed a slimy covering on floating logs. This species lives in gelatinous tubes. Scarce at Tayport.

<div align="center">Section Mesoleiae Cl.</div>

N. MINIMA Grun.; V. H. Syn. xiv, 15, 16. Loc. 42. Very abundant. With *Achnanthes minutissima* this species formed an olive-green slimy film on a porcelain sink, Greenhouse, University College, Dundee.

N. MINIMA v. ATOMOIDES Grun.; V. H. Syn. xiv, 12–14. Loc. 21, 66. Not abundant.

N. SEMINULUM Grun.; V. H. Syn. xiv, 8, 9. Loc. 14. Not abundant.

N. ROTEANA Rabh.; V. H. Syn. xiv, 17, 19. Loc. 14, 42, 66. Not abundant. I found the striae to be 24 in 10 μ. Cleve says, ' striae about 28 '.

N. BINODIS Ehb.; V. H. Syn. Suppl. pl. B. 33. Loc. 19, 52, 59. Rare.

N. MUTICA Kütz. f. COHNII Hilse; V. H. Syn. x, 17. Loc. 21, 29, 36. Not abundant.

N. MUTICA f. GOPPERTIANA Bleis.; V. H. Syn. x, 18, 19. Loc. 21, 28, 29, 36, 43, 54. Not uncommon.

N. MUTICA f. VENTRICOSA Kütz.; V. H. Syn. iv, 1 b. Loc. 36, 43. Not abundant.

N. MUTICA f. UNDULATA Hilse; V. H. Syn. x, 20 c. Loc. 36. Rare.

N. MUTICA f. GIBBOSA, f. nov. (Text-fig. 10.) Valve lanceolate, gibbous at the middle. Loc. 51. Not common. [See Appendix, p. 305.]

N. MUTICA f. ORNATA, f. nov. (Text-fig. 11.) Valve elliptic-lanceolate, gibbous at the middle, with four isolated puncta in the form of a rhombus in the central area on the side opposite the isolated punctum. Loc. 29. Not abundant. [See Appendix, p. 305.]

N. MUTICA f. QUINQUENODIS (Grun.) V. H.; V. H. Syn. x, 21. Loc. 36, 43. Not abundant. The illustration quoted above is named *N. (mutica* var. ?) *quinquenodis* Grun. (*N. nivalis* Ehb.). Cleve (Diat. of Fin. 33) refers to Van Heurck's figure, but gives another figure (ii, 5) differing in outline and absence of the punctum. Cleve gives the puncta as 18–24, Van Heurck as 15–18. Later, in his synopsis, Cleve names the diatom *N. nivalis* Ehb. (*N. quinquenodis* Grun.), omits Van Heurck's figure, but gives *N. undosa* Donk. B. D. vi, 1. In both the above collections the specimens have the distinct isolated punctum. It is evident that in such a variable species as *N. mutica* the presence or absence of the isolated punctum is of no great importance, since the only difference between *N. mutica* v. *quinquenodis* (Grun.) V. H. and *N. nivalis* Ehb., and *N. mutica* v. *ventricosa* Kütz., is the presence of this punctum.

N. MUTICA v. PULCHRA, v. nov. (Text-fig. 12.) Valve linear with triundulate margins, the middle gibbosity not more prominent than the others, ends broad, rostrate-capitate. L. 25–30 μ, b. 8–10 μ. Striae radiate, almost parallel at the ends, 18 in 10 μ, strongly punctate, puncta 12 in 10 μ. Axial area narrow but distinct, central area a broad transverse fascia, linear but widening out

slightly towards the margins, where there are very short marginal striae, area with an isolated punctum. Loc. 43. Not uncommon. [See Appendix, p. 305.]

NAVICULA BACILLIFORMIS Grun. ; Arct. Diat. ii, 51. Loc. 2, 4, 52, 55, 59, 70. Fairly common in boggy pools.

N. PUPULA Kütz. ; V. H. Syn. xiii, 15. Loc. 2, 6, 14, 52, 55, 64, 70. Abundant in Loc. 14, 52. Has the same distribution as the above, but is usually more plentiful.

N. PUPULA f. MINUTA ; V. H. Syn. xiii, 16. Loc. 26, 33, 53. Not abundant.

N. PUPULA v. RECTANGULARIS Greg. ; M. J. ii, pl. iv, 17. Loc. 58. Rare.

Section Entoleiae Cl.

N. CONTENTA Grun. v. BICEPS Arnott ; V. H. Syn. xiv, 31b. Loc. 35. Rare.

N. PERPUSILLA Grun. ; V. H. Syn. xiv, 22, 23. Loc. 16, 35, 43, 45, 46, 54, 55. One of the smallest species of *Navicula*. Common on damp rocks at : Quarry, St. Fort Estate ; Quarry, Liff ; Quarry, Birkhill ; rocks under waterfall, Kilspindie.

N. FUSIOIDES Grun. ; M. D. de Fr. x, 5, 6. Loc. 80. Rare.

Section Bacillares Cl.

N. BACILLUM Ehb. : Arct. Diat. ii, 50. Loc. 14, 23, 27, 52, 63, 65, 79. Fairly general, but never very abundant.

N. PSEUDO-BACILLUM Grun. ; Arct. Diat. ii, 52. Loc. 8, 14, 53, 58, 60, 65. Very abundant in Loc. 58, 65.

N. LAEVISSIMA (Kütz.) Grun. ; V. H. Syn. xiii, 13. Loc. 6, 53, 64. Abundant in Loc. 6.

Section Decipientes Grun.

N. SEMEN Ehb. ; A. S. Atl. lxxii, 1. Loc. 55, 58. Found only in Laird's Loch and in other collections from the Tullybaccart area. The occurrence of this species in the living state is of great interest (see p. 219).

N. INFLATA Donk. ; B. D. iii, 8. Loc. 14. Not abundant.

N. INFLATA v. ROSTRATA, v. nov. (Text-fig. 13.) Valve lanceolate with rostrate ends. L. 16–25 μ, b. 5–7 μ. S. 18 at the middle to 22–24 at the ends. Loc. 37, 57. Not very abundant. [See Appendix, p. 305.]

N. CRUCICULA W. Sm. v. OBTUSATA Grun. ; Arct. Diat. ii, 37. Loc. 10. Rare.

N. PROTRACTA Grun. ; Arct. Diat. ii, 38. Loc. 7, 8, 14, 23, 26. Not abundant. Average measurements :—L. 22–26 μ, b. 7 μ. S. 12 (to 20 at the ends).

N. INTEGRA W. Sm. ; V. H. Syn. xi, 22. Loc. 3, 14, 52, 53, 63. Not abundant.

N. SUBTILISSIMA Cl. ; Diat. of Finland, ii, 15. Loc. 52. Rare. A northern form occurring in Finland and Swedish Lapland.

Section **Fistulatae**, sect. nov.

Valves linear to linear-elliptical or lanceolate, frequently slightly gibbous at the middle ; ends obtuse, rounded, slightly rostrate or capitate ; valve crossed by delicate transverse and longitudinal ribs, between which are thin, round, membranous parts (poroids), forming transverse striae, which are either radiate throughout or become parallel towards the ends, and in the centre are more radiate and robust ; raphe straight, enclosed in a siliceous rib, from which the raphe emerges at the centre as two pipes (fistulae), which, turning towards the same side, extend to the median striae. Between the siliceous ribs a median pore, which in some specimens lengthens to a narrow canal connecting the ribs ; at the polar ends the raphe pipes turn towards the same side as the central pipes ; central area large, longitudinally elliptical or sub-rhomboidal : the striated part of the valve next the raphe is thickened and therefore slightly elevated ; this elevated part is more strongly developed round the central area and narrows to a fine line near the poles : frustule linear-elliptical to linear, with rounded ends, margins parallel or sub-parallel, slightly and abruptly convex at the middle ; girdle-bands very narrow, so that in the girdle-view the frustule is almost completely covered with transverse striae, except on the narrow bands, the valves being closely adpressed.

I have observed two distinct types of this interesting group in the district—a form in which the valve is linear-lanceolate not gibbous at the middle, striae radiate throughout, and linear-elliptical in girdle-view, and a form in which the valve is small, broadly linear, slightly or not gibbous at the middle, striae becoming parallel towards the ends, longitudinal ribs robust, in girdle-view linear with rounded ends.

The first species of this section was discovered by Lagerstedt (Sottvatt. Diat. Spetsberg. och Beeren Eiland, 30, pl. i, 7) in 1873, and named *N. gibberula* Kütz. Cleve (S. N. D. pt. 1, 140, pl. v, 17) in 1894 changed the name to *N. gibbula* Cl., giving an emended description, as the *N. gibberula* Kütz. was an entirely different species, being, in fact, a variety of *Caloneis Silicula* (*N. limosa*). Neither Lagerstedt nor Cleve gave correct figures or descriptions.

In the winter of 1922–3 I collected material from Rait, Liff, and Invergowrie containing forms of this diatom. Misled by the inaccurate figures and descriptions, I proposed to name one of these forms, and figured and described it in my manuscript, placing it systematically next to *N. gibbula* Cl. with the observation that a new section would have to be created for this distinct form. Publication of this was, of course, delayed until the completion of the present work. In May 1924 appeared ' Die Bacillariaceen-Vegetation des Sarekgebirges (Schwedish-Lappland) ' by F. Hustedt. On p. 558 appears an account of *N. gibbula* Cl. with an illustration of the middle part of the valve of the v. *capitata* Lagerst. Having had access to original specimens Hustedt was able to determine his specimens as *N. gibbula* Cl. A. Lotscher (Beitr. z. Algenfl. de Sussw. v. Westgronland, H. Bachmann, 1921) was dissatisfied with the systematic position of this species, and Hustedt, while not approving of the

constitution of a new genus, allows that a new sub-group might be formed for it, but leaves the matter for further investigation.

Having been fortunate enough to find another species closely allied to *N. gibbula*, I have formed a new section (Fistulatae) for such forms, and place it next to the section Decipientes.

The occurrence of this species, in the living state, so far south as the Sidlaws, is very remarkable (see p. 219). The type and a variety (*cantalica* Herib.) were found in the fossil deposits at Moissac, Auvergne, France, in 1903 by Heribaud.

> *a.* Valves linear-elliptical, striae radiate throughout, longitudinal ribs fine, frustule linear-elliptical.
>> *N. gibbula* Cl.
>> *N. gibbula* Cl. v. *capitata* Lagerst.
>> *N. gibbula* v. *cantalica* Herib.
> *b.* Valves linear with parallel margins or slightly gibbous at the middle, longitudinal ribs coarse, striae parallel towards the ends, frustule linear with rounded ends.
>> *N. relicta* sp. n. (*N. gibbula* v. *oblonga* Lagerst. ?).

NAVICULA GIBBULA Cl. ; S. N. D. pt. 1, 140, pl. v, 17. Loc. 36, 43. Fairly abundant in Loc. 36. Somewhat rare in Loc. 43. (Text-figs. 14 *a*, *b*.)

N. RELICTA, sp. n. (Text-figs. 15 *a*, *b*.) Valve linear, slightly narrowed towards the rounded ends. Striae 20 in 10 μ at the middle 14, radiate, but becoming parallel towards the ends, puncta (poroids) about 20 in 10 μ. Longitudinal ribs more robust than in *N. gibbula*. Frustule linear with rounded ends. L. 20–30 μ, b. 5–8 μ. Loc. 41. [See Appendix, p. 305.]

<center>Section Microstigmaticae Cl. *</center>

STAURONEIS CONSTRICTA (Ehb.) W. Sm. ; A. S. Atl. xxvi, 35–39. Loc. 9, 38, 73. Fairly abundant in Earl Grey Dock.

S. AFRICANA Cl. v. ACUMINATA Grun. ; V. H. T. No. 137. Loc. 8. Rare. L. 52 μ, b. 10 μ. S. 24.

S. GREGORII Ralfs ; V. H. Syn. Suppl. pl. B. 4. Loc. 8, 9, 64. Not uncommon.

S. ANCEPS Ehb. v. GRACILIS Cl. ; Ehb. Am. i, 14. Loc. 6. Rare.

S. ANCEPS v. BIROSTRIS Cl. ; Diat. f. Gronl. & Argent. xvi, 5. Loc. 55. Rare.

S. ANCEPS v. LINEARIS Ehb. ; V. H. Syn. iv, 7, 8. Loc. 6, 24, 36, 55, 59. Not abundant.

S. ANCEPS Ehb. v. AMPHICEPHALA Kütz. ; V. H. Syn. iv, 4, 5. Loc. 8, 14, 52, 55, 63, 69. General, but never very abundant.

S. PHOENICENTERON Ehb. v. GENUINA Cl. ; V. H. Syn. iv, 2. Loc. 2, 5, 6, 14, 26, 52, 55, 58, 60, 63, 64, 65. General in fresh water, and attaining its greatest size in still water and boggy pools. The largest specimen was found in a ditch on Tentsmuir, full of reddish iron oxide. It is unusual to find diatoms

[* The names in this section are as given by Cleve, S.N.D.]

flourishing in such a place. The maximum size given by Cleve is 150 $\mu \times 40 \mu$. Many specimens in this locality exceeded 200 μ in length, but were narrow, never reaching a breadth of 40 μ. Two specimens had the following measurements :—L. 240 μ, b. 34 μ ; S. 16 ; Puncta 12. L. 216 μ, b. 32 μ ; S. 16 ; Puncta 12.

S. PHOENICENTERON v. BRUNII Per. ; Diat. d'Auv. Herib. iii, 22. Loc. 65. Not abundant. Under the v. *genuina* Cleve includes *S. Brunii* Per. Herib. l.c., which differs in its wider axial area, stauros not linear but widening outwards, striae more radiate, and flexuose around the stauros, stauros with marginal striae of unequal length.

S. PHOENICENTERON v. AMPHILEPTA Ehb. ; Diat. d'Auv. iii, 18. Sm. B. D. xix, 186. Loc. 5, 6, 7, 14, 44, 53, 59, 66, 69. Fairly general in still waters. Cleve gives the striae and puncta as 18–21 in 10 μ. I have measured a large number of specimens from the above localities, and find the striae with few exceptions to be 16 in 10 μ. In all other respects the specimens agree with the descriptions and illustrations.

S. PARVULA Grun. v. PRODUCTA Grun. ; V. H. Syn. iv, 12. Loc. 56. Rare.

S. PARVULA v. PROMINULA Grun. ; Grun. MS. ; S. N. D. pt. 1, 149. Loc. 56, 58, 64. Rare.

S. PARVULA v. ATTENUATA, v. nov. (Text-fig. 16.) Valve linear lanceolate with attenuated or produced rostrate ends, with end diaphragms. L. 35–50 μ, b. 8–11 μ. Striae radiate 22 in 10 μ. Stauros not broad, slightly narrowed outwards. Loc. 6. Not very abundant. [See Appendix, p. 305.]

S. ACUTIUSCULA Herib. ; Diat. d'Auv. iii, 20. Loc. 10. Rare.

N. LEGUMEN Ehb. ; V. H. Syn. iv, 11. Loc. 34, 52. In slightly brackish water.

S. LEGUMEN f. PARVA ; Loc. 4, 19, 51. Not abundant.

S. SMITHII Grun. ; V. H. Syn. iv, 10. Loc. 14, 19, 52, 53, 54, 57, 59, 68 General in boggy pools.

S. JAVANICA Grun. ; A. S. Atl. pl. 241, f. 3. Loc. 55, 58. Not uncommon. The specimens agree in outline with the v. *arvernense* Herib., but have the striae and puncta of the type, i.e. 12 in 10 μ. Not hitherto recorded for Britain.

S. ACUTA W. Sm. ; V. H. Syn. iv, 3. Loc. 14, 63, 64, 68. Abundant in dam, Castle Farm, Lundie.

NAVICULA SCOPULORUM Breb. ; V. H. Syn. Suppl. pl. B, 28. Loc. 10, 80. Rather uncommon.

N. SCOPULORUM v. BELGICA V. H. ; V. H. Syn. Suppl. pl. B, 29. Loc. 80. Rare.

N. RHOMBICA Greg. ; T. M. S. iv, pl. v, fig. 1. Loc. 8, 9, 80. Fairly abundant.

NAVICULA GREVILLEI Ag.; V. H. Syn. xvi, 2. Loc. 8, 73, 80. Fairly abundant.

N. LIBELLUS Greg.: Diat. of Clyde, xiv, 101. Loc. 8. Rather uncommon.

N. COMPLANATA Grun.; A. S. Atl. xxvi, 45. Loc. 80. Rare.

N. COMPLANATA V. SUBINFLATA Grun.; A. S. Atl. xxvi, 48, 49. Loc. 80. Rare.

N. HYALOSIRA Cl.; Le Diatomiste, i, pl. xii, fig. 11. Loc. 26, 73, 80. Not abundant. Frustule very broad, and therefore seldom seen in valve view.

N. PLICATA Donk.; B. D. ix, 2. Loc. 8, 9, 10. ˙Not abundant.

N. (SCOLIOPLEURA) TUMIDA Breb. Placed in the genus *Scoliopleura* next *Scoliotropis*.

Section Minusculae Cl.

N. MINUSCULA Grun.; V. H. Syn. xiv, 3. Loc. 35. Fairly abundant.

N. BAHUSIENSIS Grun.: V. H. Syn. xiv, 2. Loc. 26, 28. Fairly abundant in both localities. This somewhat rare diatom was found by Cleve on the west coast of Sweden. The specimens which I measured had 28 striae in $10\,\mu$, not 25 as given by Cleve.

Section Decussatae Grun.

N. PLACENTA Ehb.; Donk. B. D. vi, 7. Loc. 55, 58. Not uncommon in both collections.

Section Heterostichae Cl.

N. PUSIO Cl.: S. N. D. pt. 2, pl. ii, fig. 13. Loc. 3. Not abundant. This rare species was hitherto only recorded from Rotorua Lake, New Zealand.

N. COCCONEIFORMIS Greg.; V. H. Syn. xiv, 1. Loc. 52, 53, 55, 64. Not abundant. In this district found only on the Sidlaws.

N. COCCONEIFORMIS f. PARVA, f. nov. L. $15\,\mu$, b. $8\,\mu$. Loc. 55. Not abundant. [See Appendix, p. 305.]

Section Lineolatae Cl.

N. CRYPTOCEPHALA Kütz.; V. H. Syn. viii, 1, 5. Loc. 1, 4, 7, 8, 11, 12, 16, 19, 20, 21, 24, 25, 28, 29, 32, 34, 35, 41, 44, 48, 51, 52, 54, 55, 61, 65, 74, 75, 77. One of the commonest diatoms in the district, occurring in almost 50 per cent. of the freshwater collections, and frequently very abundant. An almost pure collection was obtained at Chesterhill Pond, near Tayport.

N. CRYPTOCEPHALA v. VENETA Kütz.; V. H. Syn. viii, 3, 4. Loc. 6, 26. Not abundant. Remarkable for the rapidity of its movements.

N. CRYPTOCEPHALA v. PERMINUTA Grun.; V. H. Syn. xiv, 7. Loc. 14, 43. Not abundant.

N. CRYPTOCEPHALA v. EXILIS Kütz.; V. H. Syn. viii, 2, 4. Loc. 1, 24. Not abundant.

N. RHYNCHOCEPHALA Kütz. ; V. H. Syn. vii, **31**. Loc. 7, 8, 19, 23, 26, 29, 37, 52, 54, 55, 61, 63, 64, 79. General in fresh or slightly brackish water.

N. RHYNCHOCEPHALA V. AMPHICEROS Kütz. ; V. H. Syn. vii, **30**. Loc. 3, 5, 8. Not uncommon.

N. AVENACEA Breb. ; V. H. Syn. xv, **53**. Loc. 8, 80. Not abundant.

N. VIRIDULA Kütz. ; V. H. Syn. vii, **25**. Loc. 2, 8, 9, 11, 14, 18, 20, 21, 23, 24, 25, 26, 32, 35, 37, 43, 48, 51, 52, 54, 56, 59, 62, 63, 64, 68, 71, 75, 77, 78. The most widely distributed and most abundant species in the district. It occurs in 50 per cent. of the freshwater collections. Although almost ubiquitous in fresh water it is essentially a lowland form, and becomes quite scarce on the Sidlaws. It is remarkably constant in outline and number of striae, although in some localities the striae are faint while in others they are fairly robust. The closely allied but distinct form *N. radiosa* usually does not occur abundantly in the same localities as *N. viridula*, *N. radiosa* being much more abundant on the higher levels. *N. viridula* and *N. cryptocephala* have much the same distribution.

N. VIRIDULA V. SLESVICENSIS Grun. ; V. H. Syn. vii, **28, 29**. Loc. 1, 4, 7, 24, 25, 26, 33, 41, 54, 56, 57, 61, 63. Not so abundant as the type, with which it occurrs in six localities, while in seven localities the type is absent. This variety is usually more robustly marked than the type and in general is more abundant on the higher levels.

N. VIRIDULA V. ROSTELLATA Kütz. ; V. H. Syn. vii, **23, 24**. Loc. 5, 8, 16, 52, 53 Not abundant.

N. VULPINA Kütz. ; V. H. Syn. vii, **18**. Loc. 26, 43, 53. Not abundant.

N. HUNGARICA Grun. ; Grun. Verh. 1860, iii, 30. Loc. 1. Abundant in this locality, but not occurring elsewhere in the district. Transition forms connecting up with the var. *capitata* also occur, but the variety itself is absent.

N. HUNGARICA V. CAPITATA Ehb. ; V. H. Syn. xi, **3**. Loc. 4, 7, 23, 24, 26, 33, 35, 37, 43, 51, 52, 53, 54, 56, 59, 61, 63, 65, 71, 79. General in fresh water, occurring in almost 30 per cent. of the freshwater collections, but never very abundant.

N. CINCTA Ehb. ; V. H. Syn. vii, **13, 14**. Loc. 8, 14, 29, 36, 41, 46, 47, 53, 59. Never very abundant.

N. CINCTA V. HEUFLERI Grun. ; V. H. Syn. vii, **12, 15**. Loc. 26, 43, 78. Rather uncommon.

N. CINCTA V. LEPTOCEPHALA Breb. ; V. H. Syn. vii, **16**. Loc. 5. Rare.

N. RADIOSA Kütz. ; V. H. Syn. vii, **20**. Loc. 1, 3, 6, 13, 14, 19, 26, 44, 50, 52, 53, 55, 58, 59, 69, 78. General in fresh water. On the higher levels of the

Sidlaws specimens with alternately long and short median striae frequently occur.

NAVICULA RADIOSA v. TENELLA Breb. ; V. H. Syn. vii, 21, 22.   Loc. 15, 37, 59, 65, 66.   This variety usually does not occur with the type, and, like it, sometimes has median striae of unequal length.

N. GRACILIS Ehb. ; V. H. Syn. vii, 7, 8.   Loc. 14, 15, 20, 32, 51.   Not usually abundant.

N. GRACILIS v. SCHIZONEMOIDES V. H. ; V. H. Syn. vii, 9, 10.   Loc. 8, 38, 49, 73.   Not abundant.

N. PEREGRINA Ehb. ; A. S. Atl. xlvii, 57–60.   Loc. 8, 18, 26, 29, 38, 39. The commonest naviculoid diatom in the Tay.   Very variable and usually accompanied by some of its varieties.

N. PEREGRINA v. KEFVINGENSIS Ehb. ; A. S. Atl. xlviii, 61, 62.   Loc. 8, 9, 29, 30.   Not uncommon.

N. PEREGRINA v. PRODUCTA, var. nov.   (Text-fig. 17.)   Valve lanceolate, with produced subacute ends, which are less than 3μ broad.   Striae at the centre 6, at the ends 10, and midway 8·5 in 10μ.   Lineolae 20 in 10μ.   Central area transversely elliptical.   This variety connects up N. peregrina with N. rhynchocephala.   Loc. 27, 29.   Not very abundant.   Occurs with the type.   [See Appendix, p. 305.]

N. PEREGRINA v. MENISCUS Schum. ; V. H. Syn. viii, 19.   Loc. 8, 9.   Somewhat rare.

N. PEREGRINA v. MENISCULUS Schum. ; V. H. Syn. viii, 23, 24.   Loc. 14, 45, 48, 52, 53.   I have not found this freshwater variety occurring with the type.

N. MACULOSA Donk. ; B. D. v, 1.   Loc. 8.   Very rare.

N. TUSCULA Ehb. ; V. H. Syn. x, 14.   Loc. 14, 52, 59.   Not abundant. The structure of this and the preceding species is markedly different from that of the species with which Cleve associates them, so that Peragallo removes them to his group Stauroneidae, where they are placed beside N. mutica. Grunow remarks that the cell-contents of N. tuscula are different from those of other species of Navicula.

N. SALINARUM Grun. ; V. H. Syn. viii, 9.   Loc. 26.   Fairly abundant.

N. SALINARUM v. INTERMEDIA Grun. ; Arct. Diat. ii, 34.   Loc. 23.   Not abundant.

N. BOTTNICA Grun. ; Arct. Diat. ii, 32 ; V. H. Syn. vii, 33.   Loc. 8, 21, 26. Fairly common in the River Tay.   In Arct. Diat. the striae are given as 15 in 10μ, and in S. N. D. as 20 in 10μ, there being no correction in the corrigenda. All the River Tay specimens measured had the striae 15 or 16 in 10μ.   If the striation is as stated in the S. N. D., then the diatoms found in the localities above may be the N. solaris Greg. which Cleve says appears to be similar to

N. bottnica, but is unknown to him. Loc. 8, $42\,\mu \times 10\,\mu$; S. 15. Loc. 21, $36\,\mu \times 11\,\mu$; S. 16.

N. DIGITO-RADIATA Greg. ; V. H. Syn. vii, 4. Loc. 8. Not abundant.

N. DIGITO-RADIATA v. CYPRINUS W. Sm. ; V. H. Syn. vii, 3. Loc. 9, 10. Very abundant in loc. 10.

N. REINHARDTII Grun. ; V. H. Syn. vii, 5, 6. Loc. 1, 3, 6, 7, 13, 14, 52, 54. Fairly general in still waters.

N. REINHARDTII v. GRACILIOR Grun. ; V. H. Syn. Texte, p. 87. Loc. 14. Occurring with the type.

N. OBLONGA Kütz. ; V. H. Syn. vii, 1. Loc. 13, 14, 27, 52, 56, 70. Abundant in loc. 13, being the principal species. Not abundant in the other localities.

N. OBLONGA v. LANCEOLATA Grun. ; Verh. 1860, 523, iv, 25. Loc. 52, 56. Not abundant.

N. ARENICOLA Grun. ; Foss. Diat. Öst. Ung. xxx, 76, 77. Loc. 9. Rare.

N. DICEPHALA (Ehb.) W. Sm. ; V. H. Syn. viii, 33, 34. Loc. 7, 14, 19, 52, 53, 59. Not abundant.

N. LANCEOLATA Kütz. v. TENELLA A. S. ; A. S. Atl. xlvii, 4, 5, 46. Loc. 14. Not abundant. $30\,\mu \times 5\,\mu$. S. 18.

N. LANCEOLATA v. ARENARIA Donk. ; B. D. viii, 5. Loc. 10. Fairly abundant.

N. LANCEOLATA v. CYMBULA Donk. ; V. H. Syn. vii, 32. Loc. 53. Fairly abundant. Striae at the ends 12 in $10\,\mu$, not 10 as given by Cleve.

N. ANGLICA Ralfs ; V. H. Syn. viii, 29, 30. Loc. 1, 14. Fairly abundant in loc. 1. Somewhat rare in loc. 14.

N. ANGLICA v. SUBSALSA Grun. ; V. H. Syn. viii, 31. Loc. 7, 14. Not abundant.

N. GASTRUM Ehb. ; V. H. Syn. viii, 25, 27. Loc. 8, 56, 59, 70. Not uncommon.

N. GASTRUM v. EXIGUA Greg. ; V. H. Syn. viii, 32. Loc. 3, 8, 54, 62. Loc. 8, $16\,\mu \times 8\,\mu$. S. 14.

N. PLACENTULA Ehb. ; V. H. Syn. viii, 26, 28. Loc. 52. Fairly abundant.

N. (SCHIZONEMA) MOLLIS W. Sm. ; V. H. Syn. xv, 22, 23. Loc. 73, 80. Fairly abundant.

N. (SCHIZONEMA) RAMOSISSIMA Ag. v. GENUINA Cl. ; V. H. Syn. xv, 4, 5. Loc. 73, 80. Fairly abundant.

N. (SCHIZONEMA) RAMOSISSIMA v. AMPLIA Grun. ; V. H. Syn. xv, 3. Loc. 73, 80. Occurs with the type.

NAVICULA DIRECTA W. Sm. v. GENUINA Cl. ; W. Sm. B. D. xviii, 172. Loc. 73. Not abundant. A marine species found in northern waters. L. 60–70 μ, b. 9–10 μ. S. 9.

N. AMMOPHILA Grun. ; M. D. de Fr. xii, 13. Loc. 30. Rare. 17 $\mu \times 6 \mu$. S. 10–12 (at ends).

N. CANCELLATA Donk. ; B. D. viii, 4 *a, b*. Loc. 8, 9, 22, 73, 80. Not uncommon.

N. CANCELLATA v. GREGORII Ralfs ; A. S. Atl. xlvi, 41, 42, 71, 72. Loc. 10. Not abundant.

N. CANCELLATA v. RETUSA Breb. ; Donk. B. D. x, 3. Loc. 8, 10. Not abundant.

N. INFLEXA Greg. ; A. S. Atl. xlvi, 6, 9, 70. Loc. 8, 73. Somewhat rare.

N. NORTHUMBRICA Donk. ; B. D. viii, 1. Loc. 80. Rare.

N. FORMENTERAE C. ; S. N. D. pt. 2, pl. i, 33. Loc. 10. Rare. This species has not hitherto been recorded for Britain.

N. SOLARIS Greg. ; T. M. S. iv, pl. v, f. 10. Loc. 8, 21, 26. I have included *N. solaris* because of my inability to decide whether the striation of *N. bottnica* is as given in Arct. Diat. or in S. N. D. If as in S. N. D., then the forms found in the Tay might be the *N. solaris* of Gregory.

N. DISTANS W. Sm. ; Arct. Diat. ii, 42. (Text-fig. 18.) Loc. 8, 10, 26, 27, 29, 39, 73, 80. General in the Tay. The specimens are all slightly asymmetrical, as in the figure quoted above, which was originally called var. *borealis* Grun.

N. JAMALINENSIS Cl. ; Arct. Diat. ii, 40. Loc. 8. Rare. Not hitherto recorded in Britain.   ·

Section **Punctatae** Cl.

N. SCUTELLOIDES W. Sm. ; A. S. Atl. vi, 34. Loc. 56. Rather scarce.

N. SCUTELLOIDES v. MINUTISSIMA Cl. ; Diat. f. Gronl. och Argent. xvi, 10. Loc. 66. Rather scarce.

N. PUSILLA W. Sm. ; V. H. Syn. xi, 17. Loc. 26, 29, 39. Not abundant.

N. HUMEROSA Breb. ; V. H. Syn. xi, 20. Loc. 8, 9, 39, 80. Abundant in loc. 9, much less so in the other localities. Loc. 8, 48 $\mu \times 25 \mu$. S. 12. P. 14.

N. HUMEROSA v. ARABICA ; M. D. de Fr. xxvii, 23. Loc. 9. Rare.

N. HUMEROSA v. CONSTRICTA Cl. ; M. D. de Fr. xxvii, 21. Loc. 8, 39. Not abundant.

N. MONILIFERA Cl. ; V. H. Syn. xi, 15. Loc. 80. Somewhat rare.

N. LATISSIMA Greg. ; A. S. Atl. vi, 17. Loc. 8. Not abundant. 66 $\mu \times 41 \mu$. S. 9.

N. SERPENTINA sp. n. (Text-fig. 19.) Loc. 13. Somewhat rare. Valve broadly linear-lanceolate, with obtuse ends. L. 35–45 μ, b. 10–12 μ. Axial area moderately broad, linear, narrowed towards the ends, abruptly dilated at the middle to form a large subrhomboidal central area. Raphe oblique, flexuose. Striae 14–15 in 10 μ, slightly radiate, coarsely punctate, puncta 12 (middle) to 15 (at ends). This well-marked species resembles *N. lacustris* Greg. and *N. occidentalis* Cl., from which it differs in being narrower, in having coarser puncta, and oblique twisted raphe. [See Appendix, p. 305.]

N. PUNCTULATA W. Sm. ; V. H. Syn. xi, 16. Loc. 8. Not abundant.

N. SCANDINAVICA Lagerst. ; M. D. de Fr. xxvii, 7. Loc. 80. Rare at Carnoustie and Easthaven, but more abundant at Arbroath.

N. GRANULATA Bail. ; A. S. Atl. vi, 26, 27. Loc. 8, 10, 81. Not abundant.

Section **Lyratae** Cl.

N. HENNEDYI W. Sm. ; V. H. Syn. ix, 14. Loc. 27, 80, 81. Not abundant.

N. HENNEDYI v. MANCA A. S. ; A. S. Atl. iii, 17. Loc. 80. Rare. Previously recorded from Campeachy Bay. 112 $\mu \times 58 \mu$. S. 9. P. 12.

N. HENNEDYI v. NEBULOSA Greg. ; Diat. of Clyde, ix, 8. Loc. 8, 10. Not abundant. This variety was not found in the same collection as the type.

N. ABRUPTA Greg. ; V. H. Syn. x, 4. Loc. 8, 10, 27, 39. Fairly general in the Tay. Loc. 10. 56 $\mu \times 22 \mu$. S. 10.

N. LYRA Ehb. v. ATLANTICA A. S. ; N. S. D. i, 34. Loc. 8. Not uncommon. 51 $\mu \times 24 \mu$; S. 9. 58 $\mu \times 25 \mu$; S. 9.

N. LYRA v. CONSTRICTA Per. ; M. D. de Fr. xxiii, 3. Loc. 80. Rare. This variety is not included by Cleve.

N. PYGMAEA Kütz. ; A. S. Atl. lxx, 7. Loc. 8, 10, 27. Not uncommon.

N. FORCIPATA Grev. ; V. H. Syn. x, 3. Loc. 8, 9, 27. Not uncommon.

Section **Laevistriatae** Cl.

N. ELEGANS W. Sm. ; B. D. xvi, 137. Loc. 29. Somewhat rare.

N. ELEGANS v. CUSPIDATA Cl. ; M. D. de Fr. x, 26. Loc. 22. Somewhat rare. Previously recorded from Atlantic Coast of North America.

N. PALPEBRALIS Breb. ; V. H. Syn. xi, 9. Loc. 8, 10, 80. Not uncommon. 46 $\mu \times 14 \mu$. S. 10.

N. PALPEBRALIS v. BARCLAYANA Greg. ; V. H. Syn. xi, 12. Loc. 10. Not abundant.

N. PALPEBRALIS v. ANGULOSA Greg. ; V. H. Syn. xi, 10. Loc. 10, 27. Not abundant. 35 $\mu \times 11 \mu$. S. 10, at ends 12.

NAVICULA PALPEBRALIS V. ROBUSTA Heiden ; A. S. Atl. cclxiii, 13. Loc. 10. Not abundant.

This marine littoral species (*N. palpebralis*) is very variable, and the type is usually accompanied by several of its varieties, which themselves are linked up by intermediate or transition forms.   One of the forms occurring at Port Allen agrees with *N. solida* Cl.   Cleve (Arct. Diat.) says of *N. solida*: 'Diese mit *N. fortis* und *N. angulosa* (*N. palpebralis* v. *angulosa* Greg.) verwandte Art kommt sparlich in dem Material von Tronso vor—Taf. i, fig. 24.'   Later, however, Cleve (S. N. D.) places *N. fortis* in the Lineolatae and *N. angulosa* in the Laevistriatae.   *N. fortis* has narrow areas and lineate striae, while *N. angulosa* has an elliptical area, angular at the centre, and smooth striae. I cannot admit the species *N. solida* Cl. (which at most might be considered a variety of *N. palpebralis* closely allied to the variety *angulosa*) on the grounds of slight difference in ends and area.   The fact that the median striae are alternately longer and shorter is of no specific value, as this is found occasionally in other varieties, e.g. v. *angulosa* and v. *robusta* (vide A. S. Atl. cclxiii, 13). The affinity of *N. niceaensis* Perag. (M. D. de Fr. xi, 27) to this group is also apparent, although Peragallo says of it (l.c. p. 84) ' que je plaçais avec hésitation dans les Palpebrales '.   *N. niceaensis* is placed by Cleve amongst the Lineolatae because of its finely lineate striae.   It may therefore be considered as a link between the apparently smoothly striated species of the Laevistriatae and the lineately striated species of the Lineolatae.

ANOMOEONEIS Pfitzer.

A. SPHAEROPHORA Kütz. ; V. H. Syn. xii, 2. Loc. 13, 14, 52. Fairly abundant in loc. 13, but somewhat scarce in the other localities.

A. SPHAEROPHORA V. INTERMEDIA, var. nov. (Text-fig. 20.)   Valve elliptic-lanceolate, with rostrate-capitate ends. L. 50–70 μ, b. 16–18 μ. S. 16. Central area uniting with somewhat irregular lateral lunate areas as in *A. sculpta* Ehb. This variety is similar in shape and size to *A. sphaerophora*, but has the lateral areas of *A. sculpta*, and thus connects these two species. Occurs with the type in loc. 13 but not in 14 and 52. It is practically identical with the *A. sphaero-phora* forma of Fritsch and Rich (31), 102, fig. 4 a. [See Appendix, p. 305.]

A. BRACHYSIRA (Breb.) Grun. ; V. H. Syn. xii, 8, 9. Loc. 66, 70. Not abundant. 30 $\mu \times 8 \mu$. S. 24, not 26–7 as given by Cleve. Differs from the true *A. serians*, which has not been found in the district, by its smaller size somewhat finer striae, and more obtuse ends. Frequently the valves are slightly asymmetrical.

A. FOLLIS Ehb. ; Donk. B. D. vi, 15. Loc. 66. Rare. In the same locality occurs a form less gibbous than the type. Perhaps this is the *N. pyrenaica* W. Sm. mentioned by Cleve. This form is intermediate between *A. follis* and *A. brachysira*,

A. EXILIS (Kütz.) Grun.; V. H. Syn. xii, 11, 12. Loc. 14, 55, 66, 68, 70. Not abundant. The last three species are northern and sub-alpine forms. Their inclusion in this genus is doubtful.

FRUSTULIA Ag.

F. VULGARIS Thw.; V. H. Syn. xvii, 6. Loc. 4, 14, 19, 24, 26, 34, 48, 49, 51, 52, 56, 59, 61, 63, 64, 65, 68, 70, 71. Widely distributed in fresh water.

F. RHOMBOIDES Ehb.; V. H. Syn. xvii, 1, 2. Loc. 55, 58. Not abundant.

F. RHOMBOIDES V. AMPHIPLEUROIDES Grun.; Arct. Diat. iii, 59. Loc. 49, 52. Rare. $110\,\mu$–$120\,\mu \times 20\,\mu$–$25\,\mu$.

F. RHOMBOIDES V. SAXONICA Rabh.; Sm. B. D. xxxi, 271. Loc. 55, 66. Fairly abundant. Usually found in boggy districts.

F. RHOMBOIDES V. VIRIDULA Breb.; V. H. Syn. xvii, 3. Loc. 28, 55. Not abundant.

AMPHIPLEURA Kütz.

A. RUTILANS Trentepohl; V. H. Syn. xvi, 15, 16, 28, 38. Loc. 22, 73. General in the Tay.

A. MICANS Lyngb.; V. H. Syn. xvii, 11. Loc. 22, 38, 73. Not abundant.

A. MICANS V. FRAGILIS (Grev.) Grun.; V. H. Syn. xvi, 12. Loc. 22, 38. Not abundant.

A. PELLUCIDA Kütz.; V. H. Syn. xvii, 14, 15. Loc. 14, 52, 68, 70, 78, 80. Common in boggy districts. Very abundant in Forgan Bog. A narrow form occurs in Monikie Reservoir. 100–$120\,\mu \times 8\,\mu$.

PINNULARIA Ehb.

In the subdivision of this large genus the classification used by Cleve in the Synopsis of the Naviculoid Diatoms has been followed.

Section **Parallelistriatae** Cl.

P. GRACILLIMA Greg.; A. S. Atl. xlv, 62, 63. Loc. 14, 55, 66, 68. Not abundant. A sub-alpine form usually found in boggy pools. Loc. 14 : $26\,\mu \times 5\,\mu$; S. 22. Loc. 66 : $30\,\mu \times 5\,\mu$; S. 22.

P. LEPTOSOMA Grun.; V. H. Syn. xii, 29. Loc. 14, 34, 45. Somewhat rare.

P. MOLARIS Grun.; V. H. Syn. vi, 19. Loc. 54, 59. Somewhat rare. Found only in the Tullybaccart district.

P. ISOSTAURON (Ehb.) Grun.; Diat. d'Auv. ii, 2. Loc. 6, 52. Rare. This species is included under the section Complexae, but Cleve admits that it might better be placed here, an opinion with which I agree.

P. UNDULATA Greg.; Diat. of Finland, ii, 8. Loc. 55. Rare.

Section Capitatae C.

PINNULARIA APPENDICULATA Ag.; V. H. Syn. vi, 18, 20. Loc. 2, 14, 52, 64. Not abundant. Occurs in boggy pools.

P. SUBCAPITATA Greg.; M. J. iv, pl. i, fig. 30. Loc. 2, 5, 14, 19, 26, 36, 55, 70. Occurs in stagnant and slow-running water. Loc. 5: $35\,\mu \times 6\,\mu$; S. 12. Loc. 14: $28\,\mu \times 6\,\mu$; S. 12. Loc. 55: $40\,\mu \times 6\,\mu$; S. 12. $55\,\mu \times 6\,\mu$; S. 11.

In loc. 55 a frustule was found with dissimilar valves, only one having the stauros.

P. SUBCAPITATA v. HILSEANA f. SUBUNDULATA O. Müll.; Hoch. des Riesengeb. fig. 15. Loc. 55. Not uncommon.

P. SUBCAPITATA v. PAUCISTRIATA Grun.; V. H. Syn. vi, 23. Loc. 26, 61. Rare.

P. INTERRUPTA W. Sm. f. BICEPS Cl.; V. H. Syn. vi, 14. Loc. 6, 41, 52, 64. Not uncommon.

P. INTERRUPTA f. STAURONEIFORMIS Cl.; V. H. Syn. vi, 12, 13. Loc. 19, 26, 52, 53. Not usually found with the type.

P. MESOLEPTA Ehb.; V. H. Syn. vi, 10, 11. Loc. 14, 26, 33, 44, 50, 52, 53, 63. Fairly general in stagnant and slow-running water, but never very abundant.

P. MESOLEPTA v. STAURONEIFORMIS Grun.; A. S. Atl. xlv, 52, 53. Loc. 14, 55. Somewhat rare.

Section Divergentes Cl.

Some of the species in this section show a thickening of the silex at the middle of the valve. In *P. divergens* this siliceous thickening is most strongly developed and takes the form of a semicircular boss at the margin of the stauros. It is least developed in *P. microstauron*, in which only the margin itself is slightly thickened. In many valves of *P. Brebissonii* the striae adjacent to the stauros are markedly thickened.

P. MICROSTAURON Ehb.; V. H. Syn. vi, 9. Loc. 6, 14, 53, 55. Not uncommon. Loc. 6: $34\,\mu \times 7\,\mu$; C. 12. Loc. 14: $28\,\mu \times 6\,\mu$; C. 12. Loc. 55: $26\,\mu \times 6\,\mu$; C. 11.

I have followed O. Müller ('Bacillariales aus den Hochseen des Riesengebirges') in removing this species from the section Capitatae.

P. BREBISSONII Kütz.; V. H. Syn. v, 7. Loc. 1, 14, 52, 54, 55, 59, 63. Fairly abundant. Loc. 55: $52\,\mu \times 9\,\mu$; C. 10. $42\,\mu \times 8\,\mu$; C. 10.

P. BREBISSONII v. NOTATA Herib. & Per.; Diat. d'Auv. iv, 11. Loc. 55. Rare.

P. BREBISSONII v. DIMINUTA V. H.; V. H. Syn. v, 8. Loc. 26, 36, 41, 52, 59, 65. Does not usually accompany the type.

P. LEGUMEN Ehb.; V. H. Syn. vi, 16. Loc. 14, 55. Not abundant.

P. LEGUMEN V. FLORENTINA Herib. & Per. ; Diat. d'Auv. iv, 2. Loc. 5, 14. Rare.

P. DIVERGENS W. Sm. ; B. D. xviii, 177. Loc. 14, 55, 58, 60, 64, 66, 69, 70. Most abundant on the Sidlaws. In loc. 55 this species was in auxospore formation, and consequently a number of abnormal and post-auxospore forms occur (text-figs. 21 *a*, *b*). The predominant post-auxospore forms are linear, with rounded ends, and linear elliptical. One of the linear forms agrees with *P. parallela* Brun ('Le Diatomiste', vol. ii, xiv, 7). In the majority of these post-auxospore forms the boss of silex is not developed as in the type, and is frequently replaced by a somewhat irregular semicircle of dots on both sides of the central nodule. One of these forms is probably the forma *ornata* of Grunow. In the same collection are found specimens agreeing with the v. *sublinearis* Cl. and with the v. *elliptica* Grun. This species and *P. Legumen* are closely allied, as is borne out by the occurrence of a form (*ornata*) with the semicircular row of dots on either side of the central nodule in both species, also by a form agreeing with *P. Legumen* v. *florentina* but with the bosses of silex as in *P. divergens*. Some of the post-auxospore forms show a great likeness to *P. subsolaris* Grun.

P. DIVERGENS V. SUBLINEARIS Cl. ; A. S. Atl. xliv, 20, 23. Loc. 55. Somewhat rare.

P. DIVERGENS V. ELLIPTICA Grun. ; A. S. Atl. xliv, 6, 7. Loc. 55. Somewhat rare.

P. DIVERGENS V. ELLIPTICA f. ORNATA Grun. ; S. N. D. pt. ii, 79. Loc. 55. Rare.

P. DIVERGENTISSIMA Grun. ; V. H. Syn. vi, 32. Loc. 2, 36, 41. Not abundant

P. DIVERGENTISSIMA f. SUBACUTA, f. nov. (Text-fig. 22.) Loc. 36. Not abundant. A form with subacute ends. Occurs with the type. [See Appendix, p. 305.]

Section **Distantes** Cl.

P. BOREALIS Ehb. ; V. H. Syn. vi, 3, 4. Loc. 3, 6, 8, 14, 19, 26, 29, 36, 43, 48, 51, 52, 53, 58, 60, 63, 65, 68. General in freshwater but never abundant.

P. BOREALIS f. EVIDENTIUS PUNCTATA ; V. H. Syn. vi, 4. Loc. 68. Very rare. Only a few specimens of this rare form were found. Previously recorded by Schuman from Hohen Tatra, Austria.

P. INTERMEDIA Lagerst. ; Diat. Spets. i, 3. Loc. 26, 29, 50. Not abundant.

P. BACILLA, sp. n. (Text-fig. 23.) Valve linear, with parallel margins and rounded ends. L. 38–45 μ, b. 6–8 μ. C. 9. Axial area gradually widening from the ends to the centre, where it becomes very wide, the median striae being very short. Raphe filiform, simple, with distant central pores and hook-shaped terminal fissures somewhat distant from the ends. Striae almost parallel.

Near one end there is a bifid costa in some specimens, as in *P. borealis* f. *evidentius punctata*. This species connects *P. intermedia* and *P. borealis* with *P. parva*. Loc. 30. Not abundant. [See Appendix, p. 305.]

PINNULARIA BALFOURIANA Grun. MS.; S. N. D. pt. ii, pl. i, fig. 18. Loc. 26, 29, 58. Rare.

P. LATA Breb. v. MINOR Grun.; V. H. Syn. vi, 1, 2. Loc. 45, 52, 60, 63, 70. General but not abundant on the Sidlaws, becoming more abundant and represented by larger forms on the higher altitudes.

P. ALPINA W. Sm.; B. D. xviii, 168. Loc. 70. Not abundant. Rare in the district and occurring only on the marshy ground on the north side of Craigowl Hill, at 1,150 feet.

The last two species are typical sub-alpine forms, most abundant on boggy ground.

Section **Tabellariae** Cl.

P. STAUROPTERA Grun.; A. S. Atl. xlv, 48–50. Loc. 14, 55. Somewhat rare.

P. STAUROPTERA v. INTERRUPTA Cl.; V. H. Syn. vi, 6–8. Loc. 5, 14, 52, 55, 56, 58, 59, 63. Fairly general on the Sidlaws and much more abundant than the type.

P. STAUROPTERA v. SEMICRUCIATA Cl.; Grun. Verh. 1860, iv, 17. Loc. 14. Rare.

P. GIBBA (Ehb.) W. Sm.; B. D. xix, 180. Loc. 66. Somewhat rare. $52\,\mu \times 7\,\mu$. C. 11.

P. SUBSOLARIS Grun.; V. H. Syn. vi, 17. Loc. 52, 55. Somewhat rare.

P. STOMATOPHORA Grun.; A. S. Atl. xliv, 27–29. Loc. 2, 5, 14, 55, 58, 66, 68, 69. Not uncommon on the Sidlaws.

P. STOMATOPHORA v. CONTINUA Cl.; S. N. D. pt. ii, 83. Loc. 14, 55. Somewhat rare.

The species and the var. are sub-arctic and alpine forms.

P. TABELLARIA Ehb.; A. S. Atl. xliii, 4. Loc. 14. Somewhat rare.

P. MESOGONGYLA v. INTERRUPTA Cl.; Diat. of Finland, i, 10. Loc. 55. Rare.

Section **Brevistriatae** Cl.

P. HEMIPTERA Kütz.; A. S. Atl. xliii, 35–40. Loc. 2, 14, 52, 53, 55, 58, 66. Fairly general on the Sidlaws, but never very abundant.

P. HEMIPTERA v. INTERRUPTA Cl.; S. N. D. pt. ii, 85. Loc. 55. Not abundant.

P. ACROSPHAERIA Breb. f. GENUINA Cl.; B. D. xii, 2. Loc. 14, 52, 55, 66, 69. Not common.

P. BREVICOSTATA Cl.; A. S. Atl. xliii, 26, 27. Loc. 55. Not abundant.

P. BREVICOSTATA V. LEPTOSTAURON Cl. ; A. S. Atl. xliii, 25. Loc. 55. Rare.

P. NODOSA Ehb. f. GENUINA Cl. ; A. S. Atl. xlv, 56–57. Loc. 5, 6, 14, 45, 52, 55, 58, 59, 65, 70. Fairly general in stagnant and slowly-running water.

P. PARVA Greg. ; V. H. Syn. vi, 5. Loc. 6. Somewhat rare.

Section Majores Cl.

P. MAJOR Kütz. ; V. H. Syn. v, 3, 4. Loc. 1, 2, 5, 7, 13, 14, 23, 26, 37, 44, 52, 58, 60, 65, 70, 71, 79. General in stagnant and slowly-running water. The largest specimens occur on the Sidlaws. In loc. 55 there occurs a form which differs from the type ; valve linear, slightly gibbous at the middle and occasionally at the ends ; ends rounded, but not broadly as in *P. nobilis*. L. 250–300 μ, b. 32–35 μ. Costae 5$\frac{1}{2}$ in 10 μ. Raphe slightly complex ; central pores somewhat approximate, central nodule large, unilateral ; axial area linear, almost one-third the breadth of the valve, slightly dilated unilaterally on the same side as the central nodule. Costae slightly radiate at the middle, very slightly convergent at the ends, crossed by a narrow band one-third the width of the costae but widening towards the ends. This form differs from the type chiefly in its slightly complex raphe.

P. MAJOR V. DUBIA, var. nov. Description as above. [See Appendix, p. 306.]

P. MAJOR V. CONVERGENTISSIMA Herib. ; Diat. d'Auv. ix, 10. Loc. 14. Somewhat rare.

P. MAJOR V. TRANSVERSA A. S. ; A. S. Atl. xliii, 5, 6. Loc. 65. Not uncommon.

P. MAJOR V. HERIBAUDII, var. nov. ; *N. subacuta* Ehb. v. *minor* Herib. in Diat. Foss. d'Auv. Trois Mém. 1908, 46, pl. xiii, fig. 21. Loc. 14. Not uncommon.

P. Esox Ehb. ; Diat. d'Auv. iv, 4. Loc. 63. Not abundant.

P. Esox Ehb. v. RECTA Herib. ; Diat. Foss. d'Auv. Sec. Mém. pl. ix, fig. 22. Loc. 14. Not abundant. 100 $\mu \times$ 15 μ. C. 10.

P. WESTII, sp. n. (Text-fig. 24.) Loc. 60. Not uncommon. Valve linear, slightly narrowed towards the sub-cuneate or rounded ends ; axial area about one-third the width of the valve, gradually narrowed towards the poles. Central area a transverse fascia. Raphe slightly undulated, oblique but not complex, with large comma-shaped terminal fissures. Costae 7·5 in 10 μ, slightly radiate in the middle to slightly convergent in the ends, crossed by a band about one-third the breadth of the costae. L. 60–120 μ, b. 10–20 μ. This species resembles *P. cardinaliculus* and *P. Aestuarii*. From the former it differs in its oblique raphe, large comma-shaped terminal fissures, more distant costae, and broader band across the costae. From the latter it differs in broader band across the costae and oblique not complex raphe. I have named this species in honour of my friend Mr. George West, late lecturer, Botany Department, University College, Dundee, a diatomologist of wide experience. [See Appendix, p. 306.]

PINNULARIA DACTYLUS Ehb.; A. S. Atl. xlii, 3, 4, 5. Loc. 7, 52, 55, 58, 60, 64 65, 66, 67, 68, 69, 70. General and frequently abundant on the Sidlaw Hills in boggy pools.

P. DACTYLUS v. HORRIDA Her. & Per.; Diat. d'Auv. iv, 3. Loc. 14. Rare.

Section Complexae Cl.

P. VIRIDIS Nitzsch.; V. H. Syn. v, 5. Loc. 2, 4, 5, 6, 7, 13, 14, 19, 27, 34, 44, 52, 53, 55, 58, 59, 63, 65, 69, 70, 76. General and frequently abundant in fresh water.

P. VIRIDIS v. INTERMEDIA Cl.; A. S. Atl. xlii, 9, 10. Loc. 49. Rare.

P. VIRIDIS v. COMMUTATA Grun.; A. S. Atl. xlv, 35-37. Loc. 6, 14, 26, 51, 52, 54, 55, 58. The commonest of the varieties.

P. VIRIDIS v. LEPTOGONGYLA Grun.; A. S. Atl. xlv, 26, 28. Loc. 64. Rare.

P. VIRIDIS v. RUPESTRIS Hantzsch; A. S. Atl. xlv, 38-44. Loc. 55, 64. Not abundant. An alpine and sub-arctic form.

P. DISTINGUENDA Cl.; Diat. of Finland, i, 1. Loc. 14, 55, 58. In boggy pools. Not abundant.

P. NOBILIS Ehb.; V. H. Syn. v, 2. Loc. 5, 14, 52, 55, 58, 60, 63, 64, 67, 69. Most abundant in boggy pools. Under *P. major* Mann (*Albatross* Voy. 348) has the following remarks :—' The question of what distinction can be drawn between the above and *P. Dactylus* also *P. nobilis* is not satisfactorily answered.' Although there is considerable variation in the three species mentioned I have never experienced difficulty in determining them. Their characteristics, as defined by Cleve, mark them off as distinct species.

P. GENTILIS Donk.; B. D. xii,]. Loc. 6, 7, 14, 58, 60, 64, 66. Occurs in similar localities to the above but is not so abundant.

P. FLEXUOSA Cl.; S. N. D. pt. ii, 93, pl. i, fig. 23. Loc. 67, 70. Somewhat rare, occurring only on Auchterhouse Hill and Craigowl Hill at an altitude of over 1,000 feet. Not previously recorded for Britain.

P. STREPTORAPHE Cl.; A. S. Atl. xlii, 7. Loc. 55, 58, 64, 66, 70. Fairly abundant in boggy pools on the Sidlaws. In loc. 55 a form occurs with closer costae, less broadly rounded ends, and with the costae slightly radiate at the middle and slightly convergent at the ends. L. 208 $\mu \times 30\,\mu$. C. 6.

P. CARDINALIS Ehb.; Sm. B. D. xix, 166. Loc. 13, 52 60. Rare in the three localities.

Section Marinae Cl.

P. AMBIGUA Cl.; Cl. Vega, xxxvi, 35. Loc. 26. Rare.

P. QUADRATAREA A. S. v. SUBPRODUCTA Grun.; Arct. Diat. 28. Loc. 8. Rare. 50 $\mu \times 10\,\mu$. S. 12. Previously recorded from the Baltic.

P. CRUCIFORMIS Donk.; B. D. x, 4.   Loc. 8.   Rare.

P. RECTANGULATA Greg. v. SUBUNDULATA Grun.; Diat. of the Clyde, ix 7. Loc. 8, 10.   Rare.

P. STAUNTONII Grun.; M. D. de Fr. xi, 7.   Loc. 8, 10.   Not abundant.

SCOLIOTROPIS Cl.

S. LATESTRIATAE Breb.; V. H. Syn. xvii, 12.   Loc. 8.   Not abundant.

SCOLIOPLEURA Cl.

S. TUMIDA (Breb.) Rabh.; M. D. de Fr. xxviii, 9, 10.   Loc. 8, 39.   Somewhat rare.

TRACHYNEIS Cl.

T. ASPERA Ehb. v. GENUINA Cl.; V. H. Syn. ix, 13.   Loc. 8, 27.   Not abundant.

T. ASPERA v. INTERMEDIA Grun.; A. S. Atl. xlviii, 14.   Loc. 10, 73.   Not abundant.

T. CLEPSYDRA Donk.; B. D. x, 2.   Loc. 10.   Rare.

T. CLEPSYDRA v. SCOTICA A. S.; A. S. Atl. xlviii, 9–11.   Loc. 10.   Rare.

Family IV. **PLEUROSIGMEAE.**

TOXONIDEA Donk.

T. INSIGNIS Donk.; V. H. Syn. xvii, 10.   Loc. 80.   Rare.

T. GREGORIANA Donk.; T. M. S. vi, pl. iii, fig. 1.   Loc. 80.   Rare.

PLEUROSIGMA (Sm.) Cl.

Cleve (S. N. D. 1894, 32, 33) separates *Gyrosigma* from *Pleurosigma* of W. Sm. In the genus *Gyrosigma* he places those forms with the puncta arranged in transverse and longitudinal rows, and in the genus *Pleurosigma* those forms in which the puncta are disposed in transverse and oblique rows.   The classification of species into groups, based on the angle at which the oblique rows of puncta cross each other in *Pleurosigma*, adopted by Grunow (Arct. Diat.) and followed by Peragallo ('Le Diatomiste', 1890–1), is considered by Cleve to be artificial, and he substitutes the shape of the valve and the curve of the raphe as a basis of classification.   Later, however, Peragallo (M. D. de Fr. 156) prefers the classification of Cleve in certain groups, and suggests that *Gyrosigma* and *Pleurosigma* should be considered as subgenera.   Mann (*Albatross*, 1907, 262–3) questions the validity of the grounds on which Cleve separates these groups, and seeks to establish a close relationship between *Gyrosigma litorale* (W. Sm.) and *Pleurosigma latum* Grun., and between *G. acuminatum* Kütz. and *P. affine* Grun.   I am unable to trace any such close

affinity between these diatoms. On the whole I favour the separation of *Gyrosigma* and *Pleurosigma*, but consider them as subgenera of equal value, and would suggest the rearrangement of species in the subgenus *Pleurosigma*, so as to bring together such closely related forms as belong to the group ' Affines ' of Peragallo. The *Pleurosigma* forms are entirely marine, whereas the *Gyrosigma* forms are mostly brackish, a few being marine, and a few freshwater forms.

PLEUROSIGMA (W. Sm.) Cl.

P. NUBECULA W. Sm. ; Per. v, 23. Loc. 8. Not common. 122 $\mu \times 16 \mu$. S. T/O, 22/22.

P. CUSPIDATUM Cl. ; Per. v, 16. Loc. 8, 80. Not common. In loc. 8 a large form occurs—120 $\mu \times 28 \mu$, S. T/O, 20/21. Cleve and Peragallo give the maximum size as 100 $\mu \times 25 \mu$. Specimens of normal size occur in both collections.

P. NAVICULACEUM Breb. ; V. H. Syn. Suppl. pl. c, f. 35. Loc. 8, 80. Fairly abundant.

P. LANCEOLATUM Donk. ; Per. v, 14. Loc. 1. Rare. The more distant median striae of *P. lanceolatum* and *P. naviculaceum* indicate an affinity to *P. Normanii* Ralfs, near which species they would be more correctly placed.

P. MARINUM Donk. ; Per. iii, 11. Loc. 8, 10. Not abundant. 124 $\mu \times 29 \mu$. S. T/O, 24/22.

P. DELICATULUM W. Sm. ; Per. v, 20–22. Loc. 27, 39. Not abundant.

P. DELICATULUM V. GRACILE, var. nov.   110–125 $\mu \times 13$–16 μ. S. T/O, 25/25. Smaller and more slender than the type, with which it occurs in both localities. Occurs living at Port Allen and also in the fossil state in the clays at Invergowrie etc. [See Appendix, p. 306.]

P. ELONGATUM W. Sm. ; Per. iii, 5–8. Loc. 80. Not common. 190 $\mu \times 26 \mu$, S. T/O, 18/16.

P. SUBRIGIDUM Grun. ; Per. ii, 3. Loc. 80. Not abundant. Cleve gives as the minimum size 290 $\mu \times 28 \mu$, but all specimens measured were smaller than this :—245 $\mu \times 28 \mu$, S. T/O, 17/15 ; 250 $\mu \times 28 \mu$, S. T/O, 18/16.

P. RIGIDUM V. GIGANTEA Grun. f. MINOR ; Loc. 80. Not abundant. The specimens in the Carnoustie collection differ from the var. *gigantea* only in their smaller size :—290 $\mu \times 44 \mu$, S. T/O, 17/18 ; 320 $\mu \times 44 \mu$, S. T/O, 17/18 ; 360 $\mu \times 50 \mu$, S. T/O, 17/18.

P. NORMANII Ralfs ; Per. iv, 5, 8. Loc. 8, 27, 80. Fairly abundant.

P. NORMANII V. FOSSILIS Grun. ; Per. iv, 16–18. Loc. 27, 80. Fairly abundant. Recorded as a fossil from Virginia and Nankoori, but not previously as a living form. It is quite abundant at loc. 80. In the collections obtained at Carnoustie and Port Allen, there are numerous transition forms connecting up the type with the variety *fossilis*, and also a large number of forms exceeding

the maximum sizes given by Cleve. The following measurements of twelve specimens gives some idea of the variation in size, striation, and length–breadth ratio :—

	Transverse striae.		Oblique striae.		L/B ratio.
	Middle.	Ends.	Middle.	Ends.	
120 μ × 21 μ	20	22	16	22	6/1
120 μ × 25 μ	18	18	16	20	5/1
172 μ × 27 μ	17	18	15	19	6·5/1
180 μ × 27 μ	18	19	15	19	6·5/1
192 μ × 32 μ	17	17	13	17	6/1
208 μ × 31 μ	18	19	15	19	6·5/1
220 μ × 33 μ	17	17	14	19	6·5/1
240 μ × 38 μ	16	18	14	18	6·5/1
256 μ × 37 μ	17	18	15	17	7/1
286 μ × 38 μ	18	18	16	17	7·5/1
291 μ × 37 μ	17	18	13	18	8/1
310 μ × 38 μ	16	18	14	18	8/1

These figures show that an increase in size is accompanied by an increase in the L/B ratio. Numerous specimens of the type, variety, and transition forms are covered with short irregularly scattered spines. The L/B ratio of the transition forms is somewhat variable.

P. ANGULATUM Quekett; Per. v, 3–5. Loc. 8, 27, 80. Fairly abundant. In the Tayport collection a few strongly marked specimens occur in which the transverse and oblique striae are not equidistant.

P. ANGULATUM V. ROBUSTUM, var. nov. ; Valve as in the type, puncta more robust. 220–280 μ × 40–45 μ. S. T/O, 17/19. In addition to the above there are four well-marked varieties in the Tayport collection. In the course of my observations I have constantly met with this occurrence of a type with its varieties, particularly in the following :—*P. Normanii, P. angulatum, Navicula peregrina, Caloneis amphisboena* (brackish forms). In some species, the type is subject to considerable variation along certain lines, so that quite frequently a progressive series can be traced in which there is a gradual variation in the shape of the valve or in the striation, or in both. Many of these transition forms have been considered as varieties, but would be more correctly considered as forms. The series of transition forms between certain well established species is so complete, and the variation so small between adjacent members of the series, that it would seem that the Diatomaceae are particularly well suited for a study of variation within a species. The occurrence of transition forms is more common than is usually admitted, but, on the other hand, certain species, perhaps the great majority, have become stabilised and show little tendency to vary. [See Appendix, p. 306.]

P. ANGULATUM f. UNDULATA Grun. ; Per. v, 3. Loc. 8. Not abundant.

P. ANGULATUM V. QUADRATA W. Sm. ; Per. v, 7, 8. Loc. 8, 81. The most abundant of the varieties.

PLEUROSIGMA ANGULATUM V. STRIGOSA W. Sm. ; Per. v, 1, 2. Loc. 8. Somewhat rare.

P. ANGULATUM V. FINMARCHICA Cl. ; Grun. Arct. Diat. iii, 67. Loc. 8, 10. Somewhat rare. Not previously recorded for Britain. $160\,\mu \times 32\,\mu$. S. T/O, 17/16 ; $172\,\mu \times 32\,\mu$: S. T/O, 16/16.

P. ANGULATUM V. MINUTUM Grun. ; Per. v, 15=$P.$ minutum Grun. Loc. 8, 80. Cleve suggests that this may be a dwarf form of $P.$ angulatum v. strigosa. In the Tayport collection the var. minutum is connected to the var. strigosa by transition forms. Typical specimen : $58\,\mu \times 11\,\mu$, S. T/O, 26/28.

P. AESTUARII Breb. ; Per. v, 11-13. Loc. 8, 80. Fairly abundant.

P. RHOMBEUM Grun. ; Per. iii, 13, 14. Loc. 8, 10, 80. Somewhat rare. This species has not previously been recorded for Europe. It resembles P. angulatum and the var. quadrata, differing in the more excentric raphe and coarser striation. It occurs in the same collections as $P.$ angulatum. $114\,\mu \times 29\,\mu$, S. T/O, 17/15 ; $140\,\mu \times 34\,\mu$, S. T/O, 19/17 ; $140\,\mu \times 30\,\mu$, S. T/O, 18/16.

P. CARINATUM Donk. ; T. M. S. vi, pl. iii, 5. Loc. 8, 80. Not abundant.

P. SPECIOSUM W. Sm. ; B. D. xx, f. 197. Loc. 8, 10. Somewhat rare.

P. FORMOSUM W. Sm. ; B. D. xx, f. 195. Loc. 80. Rare.

GYROSIGMA Hassall.

G. ACUMINATUM Kütz. ; V. H. Syn. xxi, 12 ; Per. vii, 36, 37. Loc. 7, 8, 19, 23, 26, 30, 53, 56, 60, 63, 71. The commonest species of Gyrosigma occurring in fresh water. $98\,\mu \times 14\,\mu$, S. T/L, 17/17 ; $112\,\mu \times 18\,\mu$, S. T/L, 18/18 ; $115\,\mu \times 19\,\mu$, S. T/L, 18/18 ; $124\,\mu \times 15\,\mu$, S. T/L, 18/18.

G. ACUMINATUM V. NEGLECTUM, var. nov. ; Shape as in the type. L. 80–140 μ, b. 13–19 μ. S. T/L, 16/16. This variety is distinguished from the type, with which it occurs, by its coarser striation. Loc. 30, 56, 63. Not abundant. [See Appendix, p. 306.]

G. STRIGILIS W. Sm. ; Per. viii, 4, 5. Loc. 8, 27. Not abundant.

G. KÜTZINGII Grun. ; Per. viii, 22. Loc. 8, 53. Peragallo (M. D. de Fr. 171-2) makes this a variety of G. Spencerii, to which it is undoubtedly allied.

G. ATTENTUATUM Kütz. ; V. H. Syn. xxi, 11, xx, 3 ; Per. vii, 4-7. Loc. 8, 19, 26, 27, 29, 52, 60, 63, 80. Common in fresh water and frequently occurring with G. acuminatum. Loc. 29 : $160\,\mu \times 24\,\mu$, S. T/L, 14/12 ; loc. 63 : $216 \times 30\,\mu$, S., T/L, 14/10. The specimen from loc. 29 is below the minimum size given by Cleve, whilst that from loc. 63 is a large broad form. In loc. 29 a form occurs with the outline of G. attenuatum but with different striation, the transverse striae being coarser than the longitudinal—$176\,\mu \times 23\,\mu$, S. T/L, 15/16.

G. ATTENUATUM V. GIGAS, var. nov. Shape of the valve as in the type, from which it differs in size and striation. L. 300 μ–350 μ, b. 20-35 μ, S. T/L, 11-12/9-10. Loc. 60. Not very abundant, occurring with the type. [See Appendix, p. 306.]

G. ATTENUATUM v. SCALPRUM Gaill. & Turp. ; Per. vii, **3**. Loc. 8. Not abundant.

G. LITORALE W. Sm. ; Per. vii, 1. Loc. 8, 27, 28, 80. Not abundant.

G. DISTORTUM W. Sm. ; Per. viii, **32**. Loc. 8, 80. Abundant in loc. 8. Peragallo (M. D. de Fr. 173) says of this species : ' Il est vrai que Cleve donne au *G. distortum* un nombre de stries notablement inférieur à celui que j'ai trouvé.' I have carefully measured the striae on a number of specimens, and find that the striation is as described by Cleve.

G. DISTORTUM v. PARKERII Harrison ; Per. viii, **33**. Loc. 8, 27, 29, 80. Not abundant, occurs with the type.

G. DISTORTUM v. UNDULATUM, var. nov. (Text-fig. 25.) Valve linear-lanceolate, with tri-undulate margins, the ends produced to somewhat tapering obtuse ends, turned in contrary directions. L. 70–100 μ, b. 15–18 μ, S. T/L, 24/28. Loc. 8, 27. Not abundant. [See Appendix, p. 306.]

G. FASCIOLA Ehb. ; V. H. Syn. xxi, 8 ; Per. viii, 36–38. Loc. 8, 27, 80, 81. Quite abundant.

G. FASCIOLA Ehb. v. SULCATA Grun. ; V. H. Syn. xxi, 7 ; Per. viii, **43**. Loc. 8, 80. Not so abundant as the type, with which it occurs.

G. MACRUM W. Sm. ; B. D. xxxi, 276 ; Per. viii, 41. Loc. 8, 27, 80. Rare.

G. PROLONGATUM W. Sm. ; B. D. xxii, 212 ; Per. viii, 39. Loc. 8. Rare and represented only by small forms.

G. TENUISSIMUM W. Sm. ; B. D. xxii, 213 ; Per. viii, 13. Loc. 8. Rare.

G. SPENCERII W. Sm. ; V. H. Syn. xxi, 15 ; Per. viii, 8, **23**. Loc. 8, 27. Not very abundant, somewhat variable. West (British F.W. Algae, 296) says that the most abundant freshwater species of the genus are *G. attenuatum* and *G. Spencerii*. Cleve and Peragallo both give *G. Spencerii* as a brackish form. I have found it only in brackish water, and consider *G. attenuatum* and *G. acuminatum* the most abundant freshwater species.

G. SPENCERII v. EXILIS Grun. ; Per. viii, 25. Loc. 27, 80. Comparatively rare, occurs with the type.

G. SCALPROIDES v. EXIMIA Thw. ; V. H. Syn. xxi, 2. Per. viii, 27. Loc. 8, 27. Not abundant.

G. BALTICUM Ehb. ; V. H. Syn. xx, 1 ; Per. vii, 19, 20. Loc. 8, 80, 81. Very abundant in loc. 8.

G. DIMINUTUM Grun. ; Per. vii, 31, 32. Loc. 8, 26. Not abundant. Occurs with *G. balticum*, of which it is perhaps only a variety.

G. WANSBECKII Donk. ; T. M. S. vi, pl. iii, 7 ; Per. vii, 23, 24. Loc. 8, 26, 80. Fairly abundant and usually found with *G. balticum*. I have found a few specimens with the transverse and longitudinal striae equidistant. Loc. 26. 128 $\mu \times 17$ μ, S. T/L, 20/20.

GYROSIGMA (RHOICOSIGMA) ARCTICUM Cl. ; Cl. Diat. Arct. Sea, iii, 16 ; Per. x, 16, 17. Loc. 8, 26. Rare. 160 μ × 15 μ, S. T/L, 24/30.

G. (DONKINIA) RECTUM Donk.; T. M. S. vi, pl. iii, 6; Per. vii, 17. Loc. 8, 80. Not abundant.

G. (DONKINIA) v. INTERMEDIA Per. ; Per. ix, 7, 8. Loc. 8. Not abundant.

G. (DONKINIA) v. MINUTA Donk.; T. M. S. vi, pl. iii, 8; Per. ix, 9. Loc. 8. Rare. 50 μ × 11 μ, S. 20.

G. ANGUSTUM Donk. ; T. M. S. vi, pl. iii, 9 ; Per. ix, 3. Loc. 8. Not abundant.

<div align="center">Family V. AMPHITROPIDEAE.</div>

<div align="center">· AMPHIPRORA Ehb.</div>

A. PALUDOSA W. Sm. ; V. H. Syn. xxii, 10. Loc. 8, 27, 28, 80. Abundant in loc. 8 and 27. Very variable in size and form, passing by the varieties *duplex* and *hyalina* into the smaller forms of *A. alata*. The relation between the two species is well shown by specimens in loc. 8 and 80. *A. paludosa* and *A. alata* have the same distribution in the area.

A. PALUDOSA v. DUPLEX Donk. ; V. H. Syn. xxii, 15, 16. Loc. 8, 28, 80. Not abundant, occurs with the type.

A. PALUDOSA v. HYALINA Eulenst. ; V. H. Syn. xxii, 17. Loc. 8, 27, 80. Somewhat rare.

A. ALATA Kütz. ; V. H. Syn. xxii, 11, 12. Loc. 8, 10, 28, 80. Abundant in loc. 8, 80.

A. KJELLMANII Cl. v. SUBTILISSIMA V. H. ; Exped. Belg. i, 25. Loc. 80. Very rare. This is perhaps the rarest diatom in the district, and its occurrence constitutes a new record for Britain and perhaps for Europe. It was first found during the Belgian Antarctic Expedition of the *Belgica*, Collection No. 445— 'Diatomées obtenues par la fusion de neige terrestre colorée . . . . ' The specimens found at Carnoustie entirely agree with the description and figures by van Heurck. L. 60 μ, b. 23 μ. Striae on keel 15, on the valve up to 30 in 10 μ, more distant at the centre. The numerous longitudinal lines on the zone cross near the ends and the divisions are finely lineate. Its occurrence at Carnoustie may perhaps be fortuitous.

A. LATA Grev. ; S. N. D. pt. 1, pl. i, 5. Loc. 10. This somewhat rare diatom, formerly found in the Balearic Islands and in Queensland, occurs, though not abundantly, on the sands at low tide, Tayport.

A. LATA v. ANGUSTIOR, var. nov. (Text-fig. 26.) Frustule siliceous, with rounded ends, constricted at the middle. L. 90–110 μ, b. 28–32 μ, at the constriction

about 23 μ. Keel broad ; junction-line uniformly arcuate. Striae on keel and valve equidistant, 13 in 10 μ, those on the keel ending in small puncta. Connecting zone with numerous longitudinal divisions, with fine transverse striae, 20–22. Loc. 80. Somewhat rare. [See Appendix, p. 306.]

A. ROBUSTA, sp. n. (Text-fig. 27.) Frustule siliceous, strongly constricted, the margin of the keel strongly silicified. L. 85–95 μ, b. 28–32 μ. Junction-line arcuate. Striae on keel robust, 8–10 in 10 μ, on the valve very fine, 28–30, divergent. Loc. 8. Not abundant. [See Appendix, p. 306.]

AURICULA Castr.

A. DECIPIENS Grun. ; V. H. Syn. xxii, bis, 11. Loc. 8. Not abundant.

A. COMPLEXA Greg. ; Diat. of the Clyde, xii, 62. Loc. 8. Rare.

TROPIDONEIS Cl.

T. LEPIDOPTERA Greg. ; V. H. Syn. xxii, 2, 3. Loc. 10, 80. Not abundant.

T. MAXIMA v. DUBIA Cl. & Grun. ; Arct. Diat. v, 89. Loc. 8. Rare ; previously recorded from Finmark.

T. GIBBERULA Grun. ; V. H. Syn. xxii bis, 12, 13. Loc. 8, 10, 80. Not abundant.

T. PUSILLA Greg. ; Diat. of the Clyde, xii, 56. Loc. 10, 80. Rare.

T. ELEGANS W. Sm. ; V. H. Syn. xxii, 1, 6. Loc. 8, 10. Not abundant.

T. VAN-HEURCKII Grun. ; V. H. Syn. xxii bis, 6–8. Loc. 8. Rare.

T. VITREA W. Sm. ; V. H. Syn. xxii, 7–9. Loc. 8, 10, 27. Fairly abundant.

T. RECTA Greg. ; V. H. Syn. xxii bis, 9, 10. Loc. 8, 27. Not abundant. In loc. 27 occurs a form which measures : l. 90–100 μ, b. 26–29 μ, S. 21. The frustule has straighter ends and is more constricted in the middle than the type.

Family VI. CYMBELLEAE.

CYMBELLA Ag.

C. MICROCEPHALA Grun. ; V. H. Syn. viii, 36–39. Loc. 15, 16, 26, 40, 43, 46, 47, 52, 64, 70. Widespread, but never very abundant.

C. CESATII Rabh. ; V. H. Syn. viii, 35. Loc. 47. Fairly abundant. A boreal and alpine form. A number of specimens were smaller than the minimum sizes given by Cleve : 35 $\mu \times 5\cdot5$ μ, S. 18 ; 38 $\mu \times 6$ μ, S. 18.

C. ANGUSTATA W. Sm. ; B. D. xvii, 156. Loc. 46, 47, 55, 70. Somewhat rare. An arctic and alpine form.

C. DELICATULA Kütz. v. INTERMEDIA, var. nov. (Text-fig. 28.) Valve narrow, linear lanceolate, slightly asymmetrical, tapering to the sub-rostrate ends.

L. 25–35 μ, b. 5–6 μ. Axial area very narrow, indistinct, central area small. Raphe almost central, slightly arcuate. Striae slightly radiate in the middle and parallel in the ends : 16 (middle), 22 (ends) ventral ; 14 (middle), 20 (ends) dorsal. Loc. 26. Not very abundant. [See Appendix, p. 306.]

CYMBELLA AMPHICEPHALA Naegeli ; V. H. Syn. ii, 6. Loc. 2, 4, 19, 51, 53, 56, 64, 65. Fairly general in fresh water, but never very abundant.

C. LATA Grun.; S. N. D. pt. 1, pl. iv, 27. Loc. 61. Not abundant. Striae 7 (middle), 11 (ends) dorsal ; 9 (middle), 11 (ends) ventral.

C. EHRENBERGII Kütz. ; V. H. Syn. ii, 1. Loc. 13, 15, 27, 52, 56, 60. Not abundant.

C. SYMMETRICA, sp. n. (Text-fig. 29.) Loc. 52. Fairly abundant. Valve almost symmetrical, sub-lanceolate, narrow, with slightly produced sub-acute ends. L. 35–50 μ, b. 9–12 μ. Raphe almost straight and almost central ; axial area narrow, central area moderately large, orbicular. Striae radiate throughout, becoming more so towards the ends : at the middle 14 in 10 μ, at the ends 16–18, very finely lineate. The raphe ends at some distance from the polar nodules, and a spot, white or black according to the focus, appears at one side where the raphe enters the polar nodules, as in C. lapponica Cl. Polar nodules hyaline, indistinct. This species is intermediate between C. lapponica Cl. and C. stauroneiformis Lagerst. [See Appendix, p. 306.]

Judging by the locality (Sidlaw Hills) in which this species was found and from its evident close relationship to the diatoms just mentioned this is a northern form, and may possibly be a ' relicta ' species.

C. NAVICULIFORMIS Auers. ; V. H. Syn. ii, 5. Loc. 4, 6, 14, 52, 55, 56, 59, 70. Fairly general in fresh water, but never very abundant.

C. CUSPIDATA Kütz. ; V. H. Syn. ii, 3. Loc. 6, 14, 52, 53, 58, 59, 63, 67, 68. Fairly common on the Sidlaws, but never very abundant.

C. HETEROPLEURA V. MINOR Cl. ; A. S. Atl. ix, 51, 52. Loc. 14, 52. This characteristic boreal form occurs only sparingly in the two localities.

C. PROSTRATA Berk. ; V. H. Syn. iii, 9–11. Loc. 26, 71. Abundant in loc. 71.

C. VENTRICOSA Kütz. ; V. H. Syn. iii, 15, 17, 19. Loc. 3, 7, 14, 15, 17, 19, 26, 31, 35, 43, 48, 50, 51, 52, 53, 54, 55, 56, 57, 59, 61, 62, 63, 64, 65, 70, 72, 75, 78. One of the most widely distributed and most abundant of freshwater diatoms, occurring in 44 per cent. of the freshwater collections. The collection from loc. 31 consisted principally of this species, which was in the auxospore condition, and therefore contained a number of abnormal forms. The diatoms figured in V. H. Syn. pl. iii were represented, together with transition forms. Forms indented in the middle of the ventral side and agreeing with C. excisa De Toni (Boyer, Diat. Philad. xviii, 15, 19) also occur, and specimens in perfect agreement with C. philadelphica Boy. l.c. pl. xviii,. 8, which is only a sporangial form of

C. ventricosa. The diatom represented (loc. cit. fig. 15) evidently belongs to *C. ventricosa*, and shows little affinity with *C. affinis*, although Boyer, (p. 61) remarks that Cleve considers *C. excisa* as a variety of *C. affinis*. Forms abruptly gibbous at the middle of the ventral margin also occur. *C. ventricosa* is a very variable species, and is one of the diatoms most frequently found in the auxospore stage.

C. GRACILIS Rabh. ; V. H. Syn. iii, 20–23. Loc. 5, 26, 52, 53, 55, 58, 65, 66. Fairly general on the Sidlaws.

C. INCERTA Grun. ; Diat. fr. Gronl. och Argent. xvi, 12. Loc. 55, 69. Not abundant.

C. INCERTA V. NAVICULACEA Grun. ; Diat. fr. Gronl. och Argent. xvi, 11. Loc. 55, 66, 70. This and the type are sub-arctic forms and in this district are found only on the Sidlaws. The description given by Cleve in S. N. D. is inaccurate and does not agree with the original illustration. I therefore give the following emended descriptions :—*C. incerta* Grun.—Valve linear-lanceolate, tapering to the sub-obtuse ends, slightly asymmetrical etc., as in S. N. D. *C. incerta* v. *naviculacea.*—Valve linear-lanceolate, tapering to the sub-acute ends, almost naviculoid etc., as in S. N. D.

C. AEQUALIS W. Sm. ; V. H. Syn. iii, 2, 4. Loc. 14, 55, 59, 63, 70. Not abundant.

C. SINUATA Greg. ; V. H. Syn. iii, 8. Loc. 28, 53, 68. Somewhat rare.

C. TUMIDULA Grun. ; A. S. Atl. ix, 33. Loc. 70. Not abundant. The specimens were not exactly typical, being more slender and with acute ends as in the var. *salinarum.*

C. TURGIDULA Grun. ; A. S. Atl. ix, 23–26. Loc. 50. Not abundant. The two isolated puncta ending the median striae on the ventral side are very faint on some specimens but quite robust in others.

C. AFFINIS Kütz. ; V. H. Syn. ii, 19. Loc. 7, 61, 64, 70. Not abundant.

C. PARVA W. Sm. ; V. H. Syn. ii, 14. Loc. 15, 16, 17, 31, 45, 46, 47, 49, 57, 62, 68, 69. General and frequently abundant in fresh water.

C. CYMBIFORMIS Kütz. ; V. H. Syn. ii, 11. Loc. 14, 45, 52, 53, 58, 63, 65, 68, 69, 70, 78. Most abundant on the Sidlaws.

C. CISTULA Hempr. ; V. H. Syn. ii, 12, 13. (Text-fig. 30.) Loc. 3, 7, 14, 19, 26, 31, 50, 52, 53, 56, 59, 62, 63, 64, 65, 66, 68, 78. This species, which is general and abundant in fresh water, is frequently found in the auxospore stage. In collections containing auxospores cysts are found consisting of four diatoms enclosed in a gelatinous envelope. In a number of cysts it was observed that two of the diatoms had two nuclei. In specimens fixed with Flemming's solution the envelope is covered with numerous black bodies, which are undoubtedly oil-globules. I have been unable to determine the relation,

X 2

if any, of these cysts to the cysts or broods of *C. cistula* and *Synedra radians* mentioned by Smith (28) vol. ii, pp. xv, xvi. Similar cysts, but with a larger number of diatoms, were observed in *C. parva*, *Navicula cryptocephala*, and *Synedra* spp.

CYMBELLA LANCEOLATA Ehb.; V. H. Syn. ii, 7. Loc. 52, 59, 60, 61, 63, 64, 65. General but not abundant on the Sidlaws.

C. LANCEOLATA v. CORNUTA Ehb.; M. G. xv, A, f. 94. Loc. 27, 64. Rare.

C. ASPERA Ehb. (C. GASTROIDES Kütz.); V. H. Syn. ii, 8. Loc. 6, 13, 14, 45, 47, 49, 52, 55, 58, 59, 60, 63, 64, 65, 67, 68, 69, 70. General and frequently abundant in stagnant and slow-running water.

C. ASPERA Ehb. v. GIGAS, var. nov. L. 300–350 μ, b. 40–50 μ. S. 7. Puncta 10. Width of axial area 8–9 μ. Width of central area 15 μ. Loc. 14. Fairly abundant. [See Appendix, p. 307.]

C. ASPERA Ehb. v. MINOR V. H.; V. H. Syn. ii, 9. Loc. 14, 52, 70. Not abundant.

C. HELVETICA Kütz.; V. H. Syn. ii, 15. Loc. 27, 29, 45, 46, 49, 64, 70. Not abundant. A boreal and alpine form.

C. TUMIDA Breb.; V. H. Syn. ii, 10. Loc. 26. Fairly abundant.

C. TUMIDA v. FOSSILIS Grun.; Arct. Diat. 26. Loc. 26. Occurs with the type.

AMPHORA Ehb.

In this genus I have followed the classification adopted by Peragallo (M. D. de Fr. 196-7).

Amphoroidae.

I. Zone simple.

AMPHORA Cl.

A. PUSIO Cl.; S. N. D. pt. ii, pl. iii, f. 40; V. H. Diat. xxxv, 906. Loc. 26, 80. Rare. 24 μ × 15 μ, S. 14.

A. OVALIS Kütz. f. TYPICA; V. H. Syn. i, 1. Loc. 1, 2, 7, 14, 23, 30, 32, 33, 49, 51, 52, 54, 60, 61, 62, 63, 64, 65, 69, 70, 79. The commonest freshwater species of the genus, and one of the commonest of all freshwater diatoms. In loc. 49, 52, 68 abnormal forms are found sparingly which I consider to be sporangial forms of *A. ovalis*. The valves are cymbiform, with arcuate dorsal margin and almost straight ventral margin; ends obtuse, rounded. L. 55–65 μ, b. 10–12 μ, S. 14. Striae indistinctly punctate, crossed by a line running parallel to the dorsal margin. A narrow straight area runs parallel to the ventral side, but there are neither polar nodules nor raphe (text-fig. 31). These forms resemble *Amphora* sp. ? (M. D. de Fr. xlvii, 12) and have a structure similar to *Eunotia Clevei* (Diat. of Finland, 55, pl. iii, 13–16), but have not the

peculiar end-nodules of that species. *Amphora* sp. ? (M. D. de Fr. xlvi, 21) is probably a sporangial form of this or some allied species.

A. OVALIS Kütz. v. LIBYCA Ehb. ; V. H. Syn. i, 2. =*A. affinis* Kütz. Loc. 6, 13, 59, 66, 80. Occurring in fresh and brackish water, and differing from the type in having a small central area. Peragallo does not retain this variety.

A. OVALIS v. PEDICULUS Kütz. ; V. H. Syn. i, 4, 5, 6. Loc. 7, 11, 24, 56, 80. Common. Frequently occurs as an epiphyte on *Nitzschia sigmoidea* and on filamentous algae.

A. PERPUSILLA Grun. ; V. H. Syn. i, 11. Loc. 20, 25, 30, 61. Not abundant. In loc. 20, 30 the diatoms formed a lining on an iron boiler filled with water.

A. MARINA W. Sm. ; V. H. Syn. i, 16 ; A. S. Atl. xxvi, 14, 17, 18. Loc. 26, 27. Not abundant. Closely allied to *A. ovalis*, and perhaps only a brackish and marine form of that species.

A. PROTEUS Greg. ; A. S. Atl. xxvii, 3. Loc. 8, 10, 27, 39. Fairly common.

A. PROTEUS v. OCULATA Per. ; M. D. de Fr. xliv, 21, 22. Loc. 8, 39. Rare, occurring with the type.

A. ARENICOLA Grun. ; M. D. de Fr. xliv, 11–13. Loc. 27, 38. Not abundant.

A. ARENICOLA v. MINOR, var. nov. L. 25–30 μ, b. 12–14 μ, S. 14. Loc. 38. Not abundant, occurring with the type. [See Appendix, p. 306.]

II. Zone complex.

DIPLAMPHORA Cl.
(including *Calamphora* Cl.).

A. MILESIANA (Greg.) ; Diat. of the Clyde, xiii, 83. Loc. 80. Rare, found only at Carnoustie. This species, which is not included by Cleve, is considered by him to be nearly allied to *A. exsecta* Grun. Cleve mentions having seen a specimen resembling the figure in Diat. of the Clyde, from the west coast of Sweden.

Intermediae.

III. AMBLYAMPHORA Cl. (emend.).

A. ARENARIA Donk.; T. M. S. vi, pl. iii, f. 16. Loc. 9, 10, 80. Not abundant. This species presents a number of different aspects according to the way in which it is viewed.

A. ARENARIA v. DONKINII Rabh. ; Q. M. J. i, new series, i, 13. Loc. 9, 10, 80. Rare, occurring with the type.

A. ARENARIA v. RATTRAYI Cl. ; M. D. de Fr. xlviii, 17, 18. Loc. 9, 10, 80. Rare, occurring with the type.

IV. OXYAMPHORA Cl. (emend.).

AMPHORA LAEVIS Greg. ; Diat. of the Clyde, xii, 74 *a, b, c.* Loc. 80. Not abundant.

A. BACILLARIS Greg. ; Diat. of the Clyde, xiv, 100. Loc. 10, 80. Not abundant.

A. LINEOLATA (Ehb.) Grun. ; V. H. Syn. i, 13, 23. Loc. 38, 80. Not abundant. $36\,\mu \times 17\,\mu$, S. 22.

A. HYALINA Kütz. ; M. D. de Fr. 1, 7. Loc. 8, 10. Fairly common at Tayport.

Cymbelloidae.

V. Zone complex : HALAMPHORA Cl.

A. CYMBIFERA Greg. (A. TERRORIS Ehb. S. N. D. pt. 2, 122) ; Diat. of the Clyde, xiv, 97. Loc. 8, 80. Not abundant.

A. COSTATA W. Sm. ; Diat. of the Clyde, xiv, 99. Loc. 80. Not abundant.

A. COFFEAEFORMIS Ag. ; V. H. Syn. i, 19. Loc. 8, 10, 80. Fairly abundant.

A. COFFEAEFORMIS V. BOREALIS Kütz. ; V. H. Syn. i, 20. Loc. 38. Rare.

A. COFFEAEFORMIS V. ANGULARIS V. H. ; V. H. Syn. i, 21. Loc. 29. Rare.

A. SALINA W. Sm. ; B. D. xxx, 251 ; V. H. Syn. i, 19. Loc. 10, 80. Not abundant.

A. ACUTIUSCULA Kütz. ; V. H. Syn. i, 18. Loc. 10. Rare. $52\,\mu \times 6\,\mu$, S. 18.

A. EXIGUA Greg. ; Diat. of the Clyde, xii, 75. Loc. 8, 9, 73, 80. Not abundant.

A. FLUMINENSIS Grun. ; M. D. de Fr. 1, 32. Loc. 8, 10. Sometimes occurs as an epiphyte on larger diatoms, such as *Surirella gemma.* Loc. 8. L. $21\,\mu$, S. 22.

A. TURGIDA Greg. ; Diat. of the Clyde, xii, 63. Loc. 80. Rare.

VI. Zone simple : CYMBAMPHORA Cl.

A. ANGUSTA Greg. v. TYPICA Cl. ; Diat. of the Clyde, xii, 66. Loc. 80. Not abundant.

A. ANGUSTA v. VENTRICOSA Greg. ; Diat. of the Clyde, xii, 68. Loc. 10. Rare.

Family VII. GOMPHONEMEAE.

GOMPHONEMA Agardh.

G. PARVULUM Kütz. ; V. H. Syn. xxv, 9. Loc. 2, 6, 23, 33, 35, 52, 54, 56, 64, 78. Fairly general but never abundant.

G. PARVULUM v. LAGENULA Kütz. ; V. H. Syn. xxv, 8. Loc. 8. Not abundant. Cleve includes it under *G. parvulum.*

G. PARVULUM V. LANCEOLATA V. H.; V. H. Syn. xxv, 10. Loc. 44. Not abundant.

G. PARVULUM V. EXILISSIMA Grun.; V. H. Syn. xxv, 12. Loc. 50. Not abundant.

G. PARVULUM V. MICROPUS Kütz.; V. H. Syn. xxiv, 46–48, xxv, 4–6. Loc. 6, 55, 66. Fairly abundant.

G. ANGUSTATUM Kütz.; V. H. Syn. xxiv, 49, 50. Loc. 6, 16, 47, 48, 52, 54, 56, 59, 60, 66, 78. General in fresh water and frequently abundant, especially on the Sidlaws. In loc. 16, 64 I have found a number of frustules with dissimilar valves, one of the valves with striation as in the var. *producta*, and the other as in the var. *sarcophagus*.

G. ANGUSTATUM V. SARCOPHAGUS Greg.; V. H. Syn. xxv, 2. Loc. 64. Fairly abundant.

G. ANGUSTATUM V. PRODUCTA Grun.; V. H. Syn. xxiv, 52, 55. Loc. 25, 34, 36, 51, 68. Not abundant.

G. ANGUSTATUM V. SUBAEQUALIS Grun.; V. H. Syn. xxv, 1. Loc. 68. Not abundant.

G. INTRICATUM Kütz.; V. H. Syn. xxiv, 28, 29. Loc. 13, 14, 26, 52, 60, 64, 70. Not abundant.

G. INTRICATUM V. PUMILLA Grun.; V. H. Syn. xxiv, 35, 36. Loc. 14, 29, 70. Somewhat rare.

G. INTRICATUM V. FOSSILIS Pant.; A. S. Atl. ccxxxv, 1–3. Loc. 14. Not abundant. $48 \mu \times 7 \mu$, S. 10, at the middle 7–8. This variety was first found in the fossil state in Hungary.

G. INTRICATUM V. VIBRIO Ehb.; V. H. Syn. xxiv, 26, 27. Loc. 14, 66, 67. Not abundant.

G. SUBTILE Ehb.; V. H. Syn. xxiii, 13, 14. Loc. 60, 69. Not abundant.

G. GRACILE Ehb. V. AURITA Al. Br.; V. H. Syn. xxiv, 15–18. Loc. 5, 6, 14, 19, 52. Fairly abundant.

G. GRACILE V. DICHOTOMUM W. Sm.; V. H. Syn. xxv, 19–21. Loc. 14. Somewhat rare.

G. GRACILE V. NAVICULACEA W. Sm.; V. H. Syn. xxiv, 13, 14. Loc. 55. Not abundant.

G. LANCEOLATUM Ehb.; V. H. Syn. xxiv, 8–10. Loc. 6, 66. Fairly abundant.

GOMPHONEMA LANCEOLATUM V. INSIGNIS Greg.; V. H. Syn. xxiv, 39–41. Loc. 68, 70. Fairly abundant. The diatoms figured in A. S. Atlas, ccxlviii, 41, 42, occur in loc. 68. They are correctly determined by Cleve as belonging to this variety, but they are slightly abnormal, and are post-auxospore forms.

G. SUBCLAVATUM Grun.; V. H. Syn. xxiii, 39–43. Loc. 14, 43, 52, 54. Fairly abundant.

G. SUBCLAVATUM V. MONTANA Schum.; V. H. Syn. xxiii, 33–36. Loc. 5, 6, 48, 55, 68. Not abundant.

G. ACUMINATUM Ehb.; Sm. B. D. xxviii, 238a, a'. Loc. 14, 26, 37, 52. Not abundant.

G. ACUMINATUM f. BREBISSONII Kütz.; V. H. Syn. xxiii, 23–26. Loc. 14, 50, 52, 55, 59, 60, 63. Fairly abundant.

G. ACUMINATUM f. CORONATA Ehb.; V. H. Syn. xxiii, 15–17. Loc. 2, 7, 14, 19, 20, 30, 43, 44, 50, 52, 53, 55, 56, 63, 65, 66, 68, 69. General and fairly abundant.

G. ACUMINATUM f. PUSILLA Grun.; V. H. Syn. xxiii, 19. Loc. 14, 64. Somewhat rare.

G. CONSTRICTUM Ehb.; V. H. Syn. xxiii, 5, 6. Loc. 6, 7, 14, 17, 19, 20, 26, 31, 33, 43, 44, 50, 52, 53, 54, 56, 59, 62, 63, 64, 65, 66, 68. The commonest species, occurring in 30 per cent. of the freshwater collections.

G. CONSTRICTUM V. CAPITATA Ehb.; V. H. Syn. xxiii, 7–9. Loc. 26, 43, 50, 64. Occurs with the type.

G. GEMINATUM Lyngb.; Sm. B. D. xxvii, 235. Loc. 26, 39, 52, 66. Not abundant. A northern form, more or less confined to hilly districts. It occurs in the mountain burns around Loch Tay, frequently forming a thick felt-like greyish-white mass resembling sheep's wool, attached firmly to the rocks. It is rare in this district, being found in the living state only on the Sidlaws, where the specimens are of small size.

G. VENTRICOSUM Greg.; V. H. Syn. xxv, 13. Loc. 26. Somewhat rare.

G. OLIVACEUM Lyngb.; V. H. Syn. xxv, 20–27. Loc. 25, 32, 43, 48, 51, 52, 53, 54, 59, 62, 66. This stipitate species frequently occurs associated with species of *Cymbella*, forming a rich brown gelatinous covering on the stones in streams. In loc. 59 it was found in the auxospore condition. The diatom figured in A. S. Atl. ccxxxiii, 35, is an abnormal form of this species, and occurs in this collection.

G. EXIGUUM Kütz.; V. H. Syn. xxv, 35–39. Loc. 22. Rare.

Tribe 3. DIATOMEAE SURIRELLOIDAE.

Family VIII. SURIRELLEAE.

CAMPYLODISCUS Ehb.

C. HIBERNICUS Ehb. ; V. H. Syn. lxxvii, 3. Loc. 23, 37, 45, 60, 63, 68, 70, 80. Fairly general in fresh water, but never abundant. The only difference between this species and *C. noricus* lies in the latter having more numerous and more delicate ribs, and I have therefore, following Mann, included such forms with the above.

C. ECHINEIS Ehb. ; M. D. de Fr. lii, 1–5. Loc. 39. Rare.

C. HODGSONII Sm. ; M. D. de Fr. liv, 4. Loc. 39. Rare. This species and the preceding occur in the Carse clay.

C. EXIMIUS Greg. ; M. D. de Fr. liv, 1. Loc. 27, 80. Somewhat rare.

C. DECORUS Breb. ; M. D. de Fr. lvi, 23. Loc. 80. Not abundant.

C. THURETII Breb. ; M. D. de Fr. lvii, 4–9. Loc. 80. Not abundant.

SURIRELLA Turpin.

S. FASTUOSA Ehb. ; M. D. de Fr. lviii, 5, 6, 7. Loc. 8, 39. Not uncommon. A very variable species.

S. GEMMA Ehb. ; M. D. de Fr. lxviii, 4. Loc. 3, 10, 27, 81. Fairly abundant.

S. ELEGANS Ehb. ; M. D. de Fr. lxvii, 1. Loc. 52, 58, 60, 63, 69. General on the Sidlaws, but not abundant.

S. ROBUSTA Ehb. ; A. S. Atl. xxiii, 3, 4. Loc. 23, 52, 53, 55, 58, 60, 63, 71. Fairly general on the Sidlaws, but never very abundant.

S. ROBUSTA v. SPLENDIDA Ehb. ; M. D. de Fr. lxvii, 6. Loc. 14, 23, 37, 52, 63, 71, 79, 80, 81. A constituent of fresh water plankton, but also found in brackish water.

S. TENERA Greg. ; M. D. de Fr. lxvii, 5. Loc. 14, 52, 53, 65. In stagnant or slow-running water.

S. SAXONICA Auersw. ; A. S. Atl. xxii, 1, 2. Loc. 63, 65. Not abundant.

S. BISERIATA Breb. ; M. D. de Fr. lxvi, 5, 6. Loc. 54, 55, 58, 63, 64, 67, 68, 69, 70, 71. Most abundant, and attaining its greatest size on the Sidlaws. *S. biseriata* and *S. bifrons* are frequent in fresh water, the latter being more abundant in this district. West (Brit. F. W. Algae, 1904, 304) gives the size of this species as 100–170 μ. The following measurements of specimens greatly exceed the maximum :—272 $\mu \times 64 \mu$, C. 1½–2 ; 288 $\mu \times 65 \mu$, C. 1½–2. In loc. 68

the shape of many of the valves were abnormal, being rather suddenly narrowed and attenuate at one end. In loc. 70 some large specimens have a unilateral median constriction. There is considerable variation in this species in the general outline and in the shape of the ends, and some of the forms have been named *S. bifrons* Kütz.

SURIRELLA SMITHII Ralfs ; M. D. de Fr. lxv, 6, lxvi, 7.　Loc. 8, 10.　Rare.

S. LINEARIS W. Sm. ; A. S. Atl. xxiii, 27, 29, 30, etc.　Loc. 26, 27, 53, 55, 60, 63, 66, 69.　Never very abundant.

S. LINEARIS V. ELLIPTICA O. Müll. ; A. S. Atl. ccxlv, 11, 12.　Loc. 23, 53 Somewhat rare.

S. LINEARIS V. CONSTRICTA W. Sm. ; A. S. Atl. xxiii, 28.　Loc. 14, 52, 55. Not abundant.

S. LINEARIS V. AMPHIOXYS W. Sm. ; A. S. Atl. xxiii, 31, cclxxxii, 16–23. Loc. 68.　Somewhat rare.

S. HELVETICA Brun. ; A. S. Atl. cclxii, 7–9.　Loc. 14, 52, 58.　Somewhat rare.　An alpine species usually found in boggy pools.

S. OVALIS Breb. ; M. D. de Fr. lxvii, 11.　Loc. 13, 26, 30, 36.　Not abundant.

S. OVALIS V. CRUMENA Breb. ; M. D. de Fr. lxvii, 16.　Loc. 27, 32, 51, 71. Abundant in loc. 32.

S. OVALIS V. OVATA Kütz. ; M. D. de Fr. lxvii, 14, 15.　Loc. 7, 21, 24, 25, 26, 30, 32, 33, 34, 35, 48, 51, 52, 53, 57, 61, 62, 63, 74, 76, 77, 78, 79.　General in fresh water and frequently very abundant.　Occurs in 35 per cent. of the freshwater collections.　Also found in brackish water.　In loc. 74 the frustules of the living diatoms were covered with short (fungal ?) filaments.

S. OVALIS V. MINUTA Breb. ; M. D. de Fr. lxvii, 13.　Loc. 16, 23, 34, 52, 54, 57, 59, 64.　More abundant on the Sidlaws than the above varieties.

S. OVALIS V. SALINA W. Sm. ; M. D. de Fr. lxvii, 17, 18.　Loc. 8.　Somewhat rare.

S. OVALIS V. BRIGHTWELLII W. Sm. ; M. D. de Fr. lxvii, 9, 10.　Loc. 8, 27. Not abundant.

S. OVALIS V. PINNATA W. Sm. ; V. H. Syn. lxxiii, 13.　Loc. 43, 54, 59, 65. Not abundant.

S. PYRIFORMIS Kitt. ; A. S. Atl. xxiv, 14.　Loc. 8, 18, 26, 27, 28, 29, 73, 80, 81. General and fairly abundant in the Tay, being one of the characteristic diatoms of the river.　It is absent from the Carse of Gowrie clay, and therefore must be considered as a comparatively recent addition to the district.

S. SPIRALIS Kütz. ; A. S. Atl. lvi, 25, 26.　Loc. 52, 60, 64, 66, 69, 70.　General but scarce on the Sidlaws.

S. DELICATISSIMA Lewis ; A. S. Atl. cclxvi, 3–5. Loc. 66. Rare.

S. MOELLERIANA Grun. ; A. S. Atl. xxiii, 36, lvi, 21–23. Loc. 2, 14, 51, 52, 53, 59, 64, 71. Fairly well represented in the district ; most abundant on the Sidlaws.

STENOPTEROBIA Breb.

S. ANCEPS V. INTERMEDIA Lewis ; A. S. Atl. cclxxxiv, 3–5, etc. Loc. 55, 61. Fairly abundant.

CYMATOPLEURA W. Sm.

C. SOLEA W. Sm.; V. H. Syn. lv, 5–7. Loc. 7, 8, 14, 23, 27, 30, 33, 37, 52, 53, 54, 56, 58, 60, 63, 64, 65, 68, 69, 71, 79. Occurs in 30 per cent. of the freshwater collections. Frequently occurs pure, when it forms dark brown gelatinous colonies on the mud beneath still water. It is very abundant during the spring and autumn maxima, but almost disappears during the intermediate seasons. Variable in size and shape.

C. SOLEA V. APICULATA (W. Sm.) Grun. ; A. S. Atl. cclxxv, 8–10, etc. Loc. 59. Fairly abundant.

C. ELLIPTICA W. Sm. ; V. H. Syn. lv, 1. Loc. 7, 8, 14, 37, 52, 53, 60, 68, 69, 70. Fairly general in fresh water. Usually accompanies C. solea, and indeed in this district is found only with that species, but is not nearly so abundant.

C. ELLIPTICA V. NOBILIS Hantzsch. ; A. S. Atl. cclxxviii, 2, 4, 5. Loc. 23, 27. Not abundant.

C. ELLIPTICA V. HIBERNICA W. Sm. ; V. H. Syn. lv, 3, 4. Loc. 23, 52, 71. Not abundant.

Tribe 4. DIATOMEAE NITZSCHIOIDAE.

Family IX. NITZSCHIEAE.

NITZSCHIA Hassall.

Group I. **Tryblionella.**

N. GRANULATA Grun. ; V. H. Syn. lvii, 5 ; M. D. de Fr. lxix, 20. Loc. 39. Occurs in the Carse of Gowrie clay fairly abundantly. L. 15–20 μ, b. 9–12 μ. S. 8. Puncta 6.

N. NAVICULARIS Breb. ; M. D. de Fr. lxix, 21. Loc. 8, 10, 26, 27, 29, 30, 38, 39, 80. General and frequently abundant in the Tay. One of the commonest diatoms in the Carse clay.

N. PUNCTATA W. Sm. ; M. D. de Fr. lxix, 22, 24. Loc. 3, 26, 27, 39. Not abundant.

NITZSCHIA PUNCTATA V. COARCTATA Grun. ; M. D. de Fr. lxix, **26, 27**. Loc. 8. Somewhat rare.

N. TRYBLIONELLA Hantzsch ; M. D. de Fr. lxix, 6–8. Loc. 8, 27, 30. Not abundant.

N. TRYBLIONELLA V. MAXIMA Grun. ; M. D. de Fr. lxix, 2. Loc. 27. Rare.

N. TRYBLIONELLA V. LEVIDENSIS Sm. ; M. D. de Fr. lxix, 5. Loc. 8, 27, 28, 33, 38. General and fairly abundant.

N. TRYBLIONELLA V. RECTA, var. nov. (Text-fig. 32.) Valve linear, with parallel margins and cuneate ends. L. 50–60 μ, b. 8–10 μ. Keel puncta, and striae 12 in 10 μ. Loc. 8. Not abundant. [See Appendix, p. 306.]

N. TRYBLIONELLA V. SALINARUM Grun. ; M. D. de Fr. lxix, 11–13. Loc. 8. Rare.

N. DEBILIS Arnott ; M. D. de Fr. lxix, 9. Loc. 8, 19, 26, 29, 30, 33, 38, 43, 45, 52. General, but never very abundant.

N. ANGUSTATA W. Sm. ; M. D. de Fr. lxxii, 22, 23. Loc. 52, 54, 62, 65, 70. General on the Sidlaws, but not abundant.

N. MARINA Grun. ; M. D. de Fr. lxxii, 24. Loc. 10. Rare.

Group II. **Panduriformis.**

N. PANDURIFORMIS Greg. v. MINOR Greg. ; M. D. de Fr. lxx, 6. Loc. 8, 26. Somewhat rare.

N. CONSTRICTA Greg. ; M. D. de Fr. lxx, 8–10. Loc. 8, 10. Not uncommon. In loc. 8 there occurs a form larger than f. *parva*, with coarser striation : 26 $\mu \times$ 10 μ, S. 13.

N. CONSTRICTA V. SUBCONSTRICTA Grun. ; V. H. Syn. lviii, 7. Loc. 73, 80. Not abundant. In loc. 80 a form occurs with more distinct keel, puncta, and finer striation : 48 $\mu \times$ 11 μ, S. 14–15.

Group III. **Apiculatae.**

N. PLANA W: Sm. ; V. H. Syn. lviii, 10, 11. Loc. 26, 29. Not abundant.

N. ACUMINATA W. Sm. ; M. D. de Fr. lxx, 19–21. Loc. 8, 80. Not abundant.

N. ACUMINATA V. SUBCONSTRICTA Grun. ; Arct. Diat. 73. Loc. 8. Somewhat rare.

N. HUNGARICA Grun. ; M. D. de Fr. lxx, 22, 23. Loc. 29, 30, 33, 73. Fairly abundant.

N. HUNGARICA V. LINEARIS Grun. ; V. H. Syn. lviii, 23–25. Loc. 33. Somewhat rare.

N. APICULATA Greg. ; M. D. de Fr. lxx, 24, 25. Loc. 8, 9, 16, 23, 26, 27, 30, 38, 52, 73. General and fairly abundant.

Group IV. **Pseudo-Tryblionella.**

N. LITTORALIS Grun. ; M. D. de Fr. lxix, 15–18. Loc. 73. Somewhat rare.

N. LITTORALIS V. SLESVICENSIS Grun. : Arct. Diat. 76. Loc. 8. Rare.

Group V. **Circumsutae.**

Not represented in the district.

Group VI. **Dubiae.**

N. DUBIA W. Sm. ; M. D. de Fr. lxx, 30. Loc. 8, 19, 23, 26, 27, 43, 79. General and fairly abundant in the Tay.

N. COMMUTATA Grun. ; M. D. de Fr. lxx, 31. Loc. 14, 34, 54. Not abundant.

N. STAGNORUM Rabh. ; V. H. Syn. lix, 24. Loc. 26, 59. Not abundant.

N. THERMALIS Ehb. : V. H. Syn. lix, 20. Loc. 59. Not abundant.

N. THERMALIS V. LITTORALIS Grun. ; Arct. Diat. 78. Loc. 73. Not abundant.

N. THERMALIS V. LITTOREA Grun. ; V. H. Syn. lix, 21. Loc. 8, 21, 26. Not abundant.

Group VII. **Bilobatae.**

N. BILOBATA W. Sm. ; M. D. de Fr. lxx, 26. Loc. 8, 26, 29, 38, 39, 73. General and fairly abundant in the Tay. In loc. 8 large specimens occur measuring up to 200 μ, thus exceeding by 50 μ the maximum size given by other authors.

N. BILOBATA V. MINOR Grun. ; M. D. de Fr. lxx, 27. Loc. 28. Fairly abundant. 57 $\mu \times$ 13 μ, K. P. 12, S. 26 ; 65 $\mu \times$ 14 μ, K. P. 12, S. 26.

N. HYBRIDA Grun. ; M. D. de Fr. lxx, 29. Loc. 8, 27, 29, 39, 80. Not uncommon.

Group VIII. **Epithemoideae.**

Not represented in the district.

Group IX. **Grunowia.**

N. DENTICULATA Grun. ; V. H. Syn. lx, 10. Loc. 26, 53, 70, 73. Not abundant.

N. SINUATA (W. Sm.) Grun. ; V. H. Syn. lx, 11. Loc. 14, 16, 36, 43, 45, 46, 47, 52, 62, 64, 68, 70. Especially abundant on dripping wet sandstone rocks in quarries. In loc. 16 numerous abnormal post-auxospore forms were found. (Text-fig. 33 b.)

N. TABELLARIA Grun. ; V. H. Syn. lx, 12, 13. Loc. 31, 36, 51, 54. Not abundant. In loc. 36 it occurs with *N. sinuata*, to which it is connected by transition forms. It should only rank as a variety of *N. sinuata*.

Group X. **Scalares.**

NITZSCHIA SCALARIS (Ehb.) W. Sm. ; V. H. Syn. lx, 14, 15.   Loc. 27.   Rare.

Group XI. **Insignes.**

Not represented in the area.

Group XII. **Bacillaria.**

N. PARADOXA Gmel. ; M. D. de Fr. lxxii, 16.   Loc. 8, 26.   Not abundant.

N. SOCIALIS Greg. ; M. D. de Fr. lxxii, 7, 8.   Loc. 8.   Somewhat rare.

N. SOCIALIS V. BALTICA Grun. ; M. D. de Fr. lxxii, 6.   Loc. 73.   Somewhat rare.

Group XIII. **Vivaces.**

N. PETITIANA Grun. ; V. H. Syn. lxii, 6.   Loc. 8.   Not abundant.

Group XIV. **Spathulata.**

N. SPATHULATA Breb. ; V. H. Syn. lxii, 7, 8.   Loc. 8, 10.   Somewhat rare.

N. DISTANS Greg. ; V. H. Syn. lxi, 10.   Loc. 8, 10, 73.   Not abundant.

N. ANGULARIS W. Sm. ; V. H. Syn. lxii, 11–14.   Loc. 80.   Not abundant.

Group XV. **Dissipatae.**

N. DISSIPATA Grun. ; V. H. Syn. lxiii, 1.   Loc. 16, 25, 26, 35, 43, 48, 51, 56, 73.   General and frequently fairly abundant.

N. DISSIPATA Grun. v. MEDIA Grun. ; V. H. Syn. lxiii, 2, 3.   Loc. 65.   Not abundant.

N. ACULA Hantzsch ; V. H. Syn. lxiii, 4.   Loc. 50, 53.   Not abundant. Cleve (Arct. Diat. 90), De Toni (Syllog. Algar. vol. ii, 527) gives the maximum size as 106 μ, but Van Heurck (Syn. 178) gives 150 μ.   In loc. 50 a number of specimens measure 150 μ.   De Toni, Peragallo, and others give the name as ' acuta.'

Group XVI. **Sigmoideae.**

N. SIGMOIDEA W. Sm. ; V. H. Syn. lxii, 5–7.   Loc. 7, 8, 13, 14, 20, 23, 33, 43, 52, 53, 59, 60, 63, 69, 70, 71, 74, 79.   General in fresh water and frequently very abundant.   Specimens measuring 500 μ have been found in the district.

N. SIGMOIDEA v. ARMORICANA Grun. ; V. H. Syn. lxiii, 8.   Loc. 52, 63, 68, 71, 80.   Not abundant.   200 $\mu \times 12\,\mu$, K. P. 5, S. 22 ; 240 $\mu \times 12\,\mu$, K. P. 5, S. 22 ; 224 $\mu \times 12\,\mu$ K. P. 5, S. 22.   Average breadth of frustule 26 μ.

N. VERMICULARIS Hantzsch ; V. H. Syn. lxiv, 2.   Loc. 53, 60, 65, 68, 80. Fairly abundant.

N. VERMICULARIS f. MINOR V. H. ; V. H. Syn. lxiv, 1.   Loc. 32.   Somewhat rare.

N. VERMICULARIS v. LAMPROCAMPA Hantzsch ; V. H. Syn. lxiv, 3.   Loc. 50. Not abundant.

N. VERMICULARIS v. BREBISSONII W. Sm. ; V. H. Syn. lxiv, 4, 5.   Loc. 33. Not abundant.

N. MACILENTA W. Sm. ; V. H. Syn. lxiv, 6, 7.   Loc. 53, 55, 68.   Not abundant.

Group XVII. **Sigmata.**

N. SIGMA W. Sm. ; V. H. Syn. lxv, 7, 8.   Loc. 8, 27, 80.

N. SIGMA v. INTERCEDENS Grun. ; V. H. Syn. lxvi, 1.   Loc. 27.   Fairly abundant.

N. SIGMA v. RIGIDA Grun. ; V. H. Syn. lxvi, 2.   Loc. 8, 73.   Fairly abundant. Striae about 30.

N. SIGMA v. HABIRSHAWII f. BREVIOR ; V. H. Syn. lxvi, 4.   Loc. 8, 73. Not abundant.

N. SIGMA v. SIGMATELLA Grun. ; V. H. Syn. lxvi, 6.   Loc. 8.   Somewhat rare.

N. SIGMA v. RIGIDULA Grun. ; V. H. Syn. lxvi, 8.   Loc. 8, 23, 29, 34, 73. In fresh and brackish water.

N. CLAUSII Hantzsch ; V. H. Syn. lxvi, 10.   Loc. 10, 26.   Not abundant.

N. FASCICULATA Grun. ; V. H. Syn. lxvi, 11–13.   Loc. 26.   Fairly abundant.

N. (HOMAEOCLADIA) SUBCOHAERENS Grun. ; V. H. Syn. lxvi, 14.   Loc. 26. Not abundant.

N. (HOMAEOCLADIA) FILIFORMIS W. Sm. ; B. D. lv, 348.   Loc. 26.   Fairly abundant.

N. (HOMAEOCLADIA) MARTIANA Ag. ; B. D. lv, 347.   Loc. 10.   Fairly abundant.

Group XVIII. **Obtusae.**

N. OBTUSA W. Sm. ; V. H. Syn. lxvii, 1.   Loc. 5.   Rare.

N. OBTUSA v. NANA Grun. : V. H. Syn. lxvii, 3.   Loc. 26, 28.   Fairly abundant.

N. OBTUSA v. LEPIDULA Grun. ; Arct. Diat. 92.   Loc. 2.   Not abundant.

N. OBTUSA v. SCHWEINFURTHII Grun. ; V. H. Syn. lxvii, 5, 6.   Loc. 5. The principal species in the collection making up about 90 per cent. of the whole. Flourishing in ditch containing abundant growth of iron bacteria.

NITZSCHIA OBTUSA v. SCALPELLIFORMIS Grun. ; V. H. Syn. lxvii, 2. Loc. 5. Not abundant.

N. PARVULA Lewis ; A. S. Atl. cccxxxvi, 12–19. Loc. 8, 26. Fairly abundant. I agree with Hustedt that this cannot be considered as a variety of *N. obtusa*.

Group XIX. Spectabiles.

Not represented in the district.

Group XX. Lineares.

N. VITREA v. SALINARUM Grun. ; V. H. Syn. lxvii, 12. Loc. 8, 63, 78. Not abundant.

N. LINEARIS (Ag.) W. Sm. ; V. H. Syn. lxvii, 13–15. Loc. 1, 5, 11, 19, 23, 24, 33, 35. 41, 43, 45, 49, 52, 53, 59, 65, 66, 71, 79. The commonest freshwater species, and occurring in 30 per cent. of the freshwater collections.

N. LINEARIS v. TENUIS (W. Sm.) Grun. ; V. H. Syn. lxvii, 16. Loc. 6, 7, 14, 23, 30, 36, 37, 68, 69, 74. Not usually found accompanying the type.

N. RECTA Hantzsch ; V. H. Syn. lxvii, 17, 18. Loc. 7, 14, 23, 26, 50, 60, 68, 80. Never very abundant.

Group XXI. Lanceolatae.

N. LANCEOLATA W. Sm. ; V. H. Syn. lxviii, 1, 2. Loc. 73. Not abundant.

N. LANCEOLATA f. MINOR Grun. ; V. H. Syn. lxviii, 3. Loc. 28, 39, 73. Not abundant.

N. SUBTILIS Grun. ; V. H. Syn. lxviii, 7, 8. Loc. 14. Not abundant.

N. SUBTILIS v. PALEACEA Grun. ; V. H. Syn. lxviii, 9, 10. Loc. 2, 50. Not abundant.

N. BREMENSIS Hust. ; A. S. Atl. cccxxxiv, 4–10. Loc. 2, 33. Not abundant. This species was recently found at Bremen.

N. HEUFLERIANA Grun. ; V. H. Syn. lxviii, 13, 14. Loc. 64. Not abundant.

N. AMPHIBIA Grun. ; V. H. Syn. lxviii, 15–17. Loc. 24, 30, 50, 55, 78. Fairly abundant.

N. AMPHIBIA v. ACUTIUSCULA Grun. ; V. H. Syn. lxviii, 19. Loc. 14, 30, 33, 50, 59. Not abundant.

N. AMPHIBIA v. FOSSILIS ; V. H. Syn. lxviii, 24. Loc. 72. Fairly abundant. Accompanied by transition forms which connect it up with *N. Frustulum*. *N. amphibia* and *N. Frustulum* have many allied forms differing only slightly in outline and striation. Many of these have been accorded specific rank, whereas at most they are only entitled to be considered as varieties. There is

a complete series of forms from *N. amphibia* to *N. communis* Rabh., the striation of the valves becoming gradually finer. It is therefore impossible to define clearly varieties and even species.

N. CAPITELLATA Hust.; A. S. Atl. cccxlviii, 57, 59. Loc. 55. Not abundant. Recently found by Hustedt at Bremen.

N. FRUSTULUM Grun.; V. H. Syn. lxviii, 28, 29. Loc. 16, 21, 25, 35, 36, 41, 45, 47, 50, 54, 55, 72. General and frequently abundant. Average specimens measure : l. 20–30 μ, b. 3·5 μ. K. P. 9–12. S. 22-26.

N. FRUSTULUM V. PERMINUTA Grun.; V. H. Syn. lxviii, 31. Loc. 59. Not abundant.

N. FRUSTULUM V. INCONSPICUA Grun.; V. H. Syn. lxix, 6. Loc. 21, 72. Not abundant.

N. FRUSTULUM V. TENELLA Grun.; V. H. Syn. lxix, 30. Loc. 6. Not abundant.

N. FRUSTULUM V. PERPUSILLA Rabh.; V. H. Syn. lxix, 8. Loc. 14, 50. Fairly abundant.

N. HANTZSCHIANA Rabh.; V. H. Syn. lxix, 1. Loc. 36, 43, 59. Not abundant.

N. INTERMEDIA Hantzsch ; V. H. Syn. lxix, 10. Loc. 5, 37, 53, 72. Not uncommon.

N. TUBICOLA Grun.; V. H. Syn. lxix, 14. Loc. 41. Rare.

N. FONTICOLA Grun. : V. H. Syn. lxix, 15-19. Loc. 41, 65, 72, 80. Not abundant.

N. PALEA W. Sm.; V. H. Syn. lxix, 22 *b*. Loc. 4, 6, 7, 12, 22, 24, 28, 30, 32, 35, 64, 75. General and freqently abundant. Somewhat variable.

N. PALEA V. MINUTA Bleisch : V. H. Syn. lxix, 23. Loc. 23. Not abundant.

N. PALEA V. KUETZINGIANA Hilse ; V. H. Syn. lxix, 24–26. Loc. 6, 21. Not abundant.

N. PALEA V. DEBILIS Grun.; V. H. Syn. lxix, 28, 29. Loc. 5, 41. Not abundant.

N. PALEA V. TENUIROSTRIS Grun.; V. H. Syn. lxix, 31. Loc. 49. Not abundant.

N. COMMUNIS Rabh.; V. H. Syn. lxix, 32. Loc. 1, 2, 16, 24. Fairly abundant.

N. COMMUNIS V. ABBREVIATA Grun.; V. H. Syn. lxix, 35. Loc. 35. Not abundant.

Group XXII. Nitzschiella.*

N. LONGISSIMA Ralfs ; V. H. Syn. lxx, 1, 2. Loc. 81. Not abundant.

NITZSCHIA CLOSTERIUM W. Sm.; V. H. Syn. lxx, 5. Loc. 2, 8, 26, 27, 29. Fairly abundant in brackish water.

N. ACICULARIS W. Sm.; V. H. Syn. lxx, 6. Loc. 4, 11, 33, 36, 76. Frequently abundant in ponds and ditches. Exhibits very rapid and jerky movements.

N. LORENZIANA v. SUBTILIS Grun.; Arct. Diat. 102. Loc. 8. Not abundant.

HANTZSCHIA Grun.

H. AMPHIOXYS Grun.; M. D. de Fr. lxxi, 14. Loc. 6, 14, 17, 19, 20, 30, 32, 33, 34, 36, 41, 43, 45, 46, 52, 53, 54, 58, 63. General and frequently abundant in fresh water, occurring in almost 30 per cent. of the freshwater collections. Very variable.

H. AMPHIOXYS v. MAJOR Grun.; M. D. de Fr. lxxi, 15. Loc. 8, 36, 59. Not abundant.

H. AMPHIOXYS v. INTERMEDIA Grun.; M. D. de Fr. lxxi, 17. Loc. 36, 52, 68. Fairly abundant.

H. AMPHIOXYS v. LANCEOLATA, var. nov. (Text-fig. 34.) L. 50–60 μ, b. 6–8 μ. Valve sub-lanceolate, with a slight median constriction on the dorsal side. Ends capitate. Keel puncta 10–11. Striæ 22, finely punctate, parallel, convergent at the ends. Loc. 36. Not abundant, but by no means rare. [See Appendix, p. 307.]

H. AMPHIOXYS v. ELONGATA Grun.; V. H. Syn. lvi, 7, 8. Loc. 36. Not abundant.

H. AMPHIOXYS v. RUPESTRIS Grun.; V. H. Syn. lvi, 9, 10. Loc. 36, 64. Fairly abundant.

H. AMPHIOXYS f. CAPITELLATA Hust.; A. S. Atl. cccxxix, 9. Loc. 45. Not abundant.

H. AMPHIOXYS f. CAPITATA O. Müll.; A. S. Atl. cccxxix, 13, 14. Loc. 58, 60. Not abundant.

H. VIRGATA Grun.; M. D. de Fr. lxxi, 18. Loc. 9, 80. Not abundant.

H. MARINA Grun.; M. D. de Fr. lxxi, 19. Loc. 8, 9. Not uncommon.

H. RIGIDA, sp. n. (Text-fig. 35.) Loc. 10. Not abundant. Valve almost straight; dorsal margin slightly concave at the middle; ventral margin convex; ends straight, produced, linear, about 6 μ long. L. 40–50 μ, b. 6–7 μ. Striæ 16, punctate, parallel; keel puncta 7, elongated, the middle two more distant than the others. [See Appendix, p. 307.]

DENTICULA Kütz.

D. TENUIS Kütz.; V. H. Syn. xlix, 28–31. Loc. 16, 26, 33, 43, 46, 49, 51, 53, 78. Fairly general, but never very abundant.

D. TENUIS v. INTERMEDIA Grun.; V. H. Syn. xlix, 22. Loc. 28, 67. Not abundant.

D. TENUIS v. INFLATA Grun.; V. H. Syn. xlix, 32–34. Loc. 46, 52, 55. Not abundant.

D. TENUIS v. FRIGIDA Grun.; V. H. Syn. xlix, 35–38. Loc. 52, 55, 67. Not abundant.

D. SUBTILIS Grun.; V. H. Syn. xlix, 10–13. Loc. 29. Somewhat rare.

PSEUDO-NITZSCHIA Per.

NITZSCHIA SERIATA Cl.; M. D. de Fr. lxxii, 28. Loc. 81. In tow-nettings of the Tay.

N. DELICATISSIMA Cl.; Gran. Nord. Plankton, 130. Loc. 81. In tow-nettings of the Tay.

Family X. EPITHEMIEAE.

RHOPALODIA Müller (emend. Per.).

R. GIBBA Kütz.; V. H. Syn. xxxii, 1, 2. Loc. 14, 46, 52, 55, 64, 65, 67, 68, 69, 70. Common in fresh and less common in brackish water. The largest specimens were found in stagnant water, e.g. Forgan Bog.

R. GIBBA v. PARALLELA Grun.; V. H. Syn. xxxii, 3. Loc. 68. Not abundant.

R. GIBBA v. VENTRICOSA Kütz.; V. H. Syn. xxxii, 4, 5. Loc. 6, 13, 52, 55, 64, 66, 68. Fairly abundant. Frequently occurs with the type.

R. GIBBERULA Kütz. v. RUPESTRIS Grun.; W. Sm. B. D. i, 12. Loc. 14, 53, 55, 58, 59, 66, 69, 70. Frequently abundant on the Sidlaws.

EPITHEMIA Breb.

E. TURGIDA Kütz.; V. H. Syn. xxxi, 1, 2. Loc. 13, 14, 39, 52, 64, 65. Frequently abundant in stagnant water. Occurs sparingly in the Carse clay.

E. TURGIDA v. WESTERMANNII Kütz.; V. H. Syn. xxxi, 8. Loc. 52, 65, 68, 70. Not abundant. In loc. 70 a number of specimens (valves) were found with one end shaped as in this variety and the other end as in the type.

E. TURGIDA v. GRANULATA Kütz.; V. H. Syn. xxxi, 5, 6. Loc. 13, 58, 59, 64, 66, 67, 68, 70. More abundant than the type and with a similar distribution.

E. TURGIDA v. CAPITATA Fricke; A. S. Atl. ccl, 1. Loc. 70. Somewhat rare.

E. HYNDMANNII W. Sm.; Sm. B. D. i, 1. Loc. 39, 60. Rather uncommon. Mann (*Albatross* Voy. p. 378) says : ' There is a very close similarity between

the present species [*turgida*] and *Ep. Hyndmannii*, so much so that their separation, although upheld by De Toni and others, appears to me decidedly doubtful. In fact my specimen is about midway between the two, having the strongly bowed dorsal outline and broad rounded apices of *Ep. Hyndmannii* together with the beading of *Ep. turgida*, especially the large beading along the ventral margin as seen in the zonal view.' I have found such forms in the district.

EPITHEMIA SOREX Kütz.; V. H. Syn. xxxii, 6–10. Loc. 13, 15. Not abundant.

E. ARGUS Kütz.; V. H. Syn. xxxi, 15–17. Loc. 15, 52, 60, 70. Not abundant.

E. ARGUS v. AMPHICEPHALA Grun. (E. ALPESTRIS W. Sm.); V. H. Syn. xxxi, 19. Loc. 52, 55, 58, 64. A sub-alpine form fairly abundant on the Sidlaws.

E. ARGUS v. LONGICORNIS Grun.; Sm. B. D. xxx, 24. Loc. 15. Rare.

E. ZEBRA Kütz.; V. H. Syn. xxxi, 9, 11–14. Loc. 14, 55, 59, 60, 64, 68. Founded in stagnant and slow-running water.

E. ZEBRA v. PROBOSCIDEA Grun.; V. H. Syn. xxxi, 10. Loc. 52. Not abundant.

E. MUELLERI Fricke; A. S. Atl. ccli, 22. Loc. 70. Somewhat rare. This species has the appearance of a post-auxospore form.

CERATONEIS Kütz.

C. ARCUS Kütz.; V. H. Syn. xxxvii, 7. Loc. 26, 27, 28, 66, 73. In four of the above localities the presence of this species is accidental—it being typically a sub-alpine form—the diatoms having been brought down from the upper reaches of the Tay. It occurs sparingly on Auchterhouse Hill.

EUNOTIA Ehb.

E. PECTINALIS Rabh.; A. S. Atl. cclxxi, 10, 11, 15. Loc. 14. Somewhat rare.

E. PECTINALIS v. IMPRESSA O. Müll.; V. H. Syn. xxxv, 1. Loc. 44, 55. Not abundant. =*E. impressa* v. *angusta* Grun.

E. PECTINALIS v. MINOR (Kütz.) Rabh.; V. H. Syn. xxxiii, 18, 20, 21. Loc. 14, 45. Not uncommon. Forma *curta* O. Müll. and var. *stricta* Rabh. are included here.

E. GRACILIS Rabh.; V. H. Syn. xxxiii, 1, 2. Loc. 2, 14, 52, 55, 56, 63, 66, 68, 70. General in fresh water, but not abundant.

E. LUNARIS (Ehb.) Grun.; V. H. Syn. xxxv, 3, 4. Loc. 2, 3, 6, 13, 14, 40, 55, 56, 59, 61, 63, 64, 66, 68, 70. General in fresh water and sometimes fairly abundant.

E. LUNARIS f. MAJOR Grun.; V. H. Syn. xxxv, 6 a. Loc. 14, 52. Not abundant.

E. LUNARIS v. BILUNARIS Grun.; V. H. Syn. xxxv, 6 b. Loc. 26. Somewhat rare.

E. LUNARIS v. EXCISA Grun.; V. H. Syn. xxxv, 6 c. Loc. 6, 26. Not abundant.

E. PRAERUPTA Ehb.; V. H. Syn. xxxiv, 19. Loc. 70. Not abundant.

E. PRAERUPTA v. CURTA Grun.; V. H. Syn. xxxiv, 23, 24. Loc. 55, 68, 69. Not abundant, but more common than the type.

E. PRAERUPTA v. BIDENS Grun.; V. H. Syn. xxxiv, 20. Loc. 55, 68. Not abundant.

E. ARCUS Ehb.; V. H. Syn. xxxiv, 2. Loc. 14, 52, 66, 70. Not abundant.

E. ARCUS v. MINOR Grun.; V. H. Syn. xxxiv, 3. Loc. 14, 55, 68. Not abundant.

E. ARCUS v. UNCINATA Grun.; V. H. Syn. xxxiv, 13. Loc. 52. Rare.

E. EXIGUA Breb.; V. H. Syn. xxxiv, 11. Loc. 66, 70. Somewhat rare.

E. PARALLELA Ehb. f. ANGUSTIOR Grun.; V. H. Syn. xxxiv, 16. Loc. 68. Rare.

E. MAJOR (W. Sm.) Rabh.; V. H. Syn. xxxiv, 14. Loc. 52. Rare.

E. MONODON Ehb.; V. H. Syn. xxxiii, 3. Loc. 14. Rare.

E. MONODON f. CURTA Grun.; V. H. Syn. xxxiii, 4. Loc. 52, 68. Not abundant.

E. DIODON Ehb.; V. H. Syn. xxxiii, 5, 6. Loc. 26, 52, 58, 68. Not abundant. Includes the f. *minor*.

E. TRIDENTULA Ehb. v. PERPUSILLA Grun.; V. H. Syn. xxxiv, 31. Loc. 66, 67. Not abundant. In loc. 67 there occurs a form with four teeth—f. *quatuor dentatae*.

E. ROBUSTA Ralfs v. TETRAODON Ehb.; V. H. Syn. xxxiii, 11. Loc. 52, 56. Not abundant.

E. FLEXUOSA (Breb.) Kütz.; V. H. Syn. xxxv, 9. Loc. 26, 68. Not abundant.

PSEUDO-RAPHIDEAE.

Tribe 5. DIATOMEAE FRAGILAROIDAE.

Family XI. SYNEDREAE.

SYNEDRA Ehb.

Subgenus EUSYNEDRA.

S. PULCHELLA Kütz.; V. H. Syn. xl, 28, 29. Loc. 8, 28. Fairly abundant.

S. PULCHELLA f. MAJOR; V. H. Syn. xl, 27, xli, 1. Loc. 50. Not abundant.

S. PULCHELLA v. SMITHII Ralfs; V. H. Syn. xli, 2. Loc. 26, 40. Not abundant.

S. PULCHELLA v. LANCEOLATA O'Meara; V. H. Syn. xli, 7. Loc. 27. Fairly abundant.

S. VAUCHERIA Kütz.; V. H. Syn. xl, 19. Loc. 7, 24, 25, 56, 59, 64. Fairly abundant.

S. VAUCHERIA v. PERMINUTA Grun.; V. H. Syn. xl, 23. Loc. 59. Somewhat rare. Occurs with the type.

S. VAUCHERIA v. CAPITELLATA Grun.; V. H. Syn. xl, 26. Loc. 26. Not abundant.

S. ULNA (Nitzsch) Ehb.; V. H. Syn. xxxviii, 7. Loc. 7, 11, 16, 17, 19, 20, 24, 43, 46, 48, 49, 51, 53, 55, 56, 59, 61, 62, 65, 67, 68, 69, 70, 71. General, and frequently abundant in fresh water. Occurs in about 40 per cent. of the freshwater collections.

S. ULNA v. SPLENDENS V. H.; V. H. Syn. xxxviii, 2. Loc. 14, 63. Not abundant.

S. ULNA v. LONGISSIMA V. H.; V. H. Syn. xxxviii, 3. Loc. 11. Fairly abundant. L. 400–450 μ.

S. ULNA v. SPATHULIFERA Grun.; V. H. Syn. xxxviii, 4. Loc. 19, 46. Not abundant.

S. ULNA v. DANICA V. H.; V. H. Syn. xxxviii, 14a. Loc. 3, 6, 11, 13, 26, 30, 44, 50, 55, 59, 63, 64. General, and frequently abundant.

S. ULNA v. OBTUSA V. H.; V. H. Syn. xxxviii, 6. Loc. 11, 26. Not abundant.

S. BICEPS Kütz.; A. S. Atl. ccciii, 10–15. Loc. 61. Not abundant. De Toni says of this 'Videtur Eunotiae sp.'. The figures referred to above represent a large diatom allied to the large forms of S. ulna.

S. ACUS (Kütz.) Grun.; V. H. Syn. xxxix, 4. Loc. 3, 17, 63, 64. Not uncommon.

S. ACUS v. DELICATISSIMA Grun. ; V. H. Syn. xxxix, 7. Loc. 44, 56, 59. Not uncommon.

S. RADIANS (Kütz.) Grun. ; V. H. Syn. xxxix, 11. Loc. 50, 70. Not abundant.

S. GAILLIONII Ehb. ; V. H. Syn. xxxix, 18. Loc. 8, 80. Fairly abundant at Tayport and Carnoustic.

S. INVESTIENS W. Sm. ; V. H. Syn. xl, 3. Loc. 18. On *Ectocarpus* at Woodhaven.

S. FAMILIARIS Kütz. et f. PARVAE MAJORESQUE ; V. H. Syn. xl, 15, 16. Loc. 2. Abundant. Attached to *Cladophora flavescens* in stagnant water, grouse drinking-hole, Tentsmuir.

S. CAPITATA Ehb. ; V. H. Syn. xxxviii, 1. Loc. 50, 58, 60, 63, 65. Found only on the Sidlaws.

S. AMPHICEPHALA Kütz. ; V. H. Syn. xxxix, 14. Loc. 70. Not abundant.

S. AFFINIS Kütz. ; V. H. Syn. xli, 13. Loc. 18, 20, 26, 30, 38. Fairly abundant.

S. AFFINIS v. HYBRIDA V. H. ; V. H. Syn. xli, 9*b*, 10. Loc. 8, 73. Not abundant.

S. AFFINIS v. GRACILIS V. H. ; V. H. Syn. xli, 15*c*. Loc. 11, 40. Not uncommon.

S. AFFINIS v. FASCICULATA V. H. ; V. H. Syn. xli, 15*a*, *b*. Loc. 21, 22, 80. Fairly abundant.

S. AFFINIS v. PARVA Kütz. ; V. H. Syn. xli, 23. Loc. 18, 26, 30. Not abundant.

Subgenus ARDISSONIA De Not.

S. FORMOSA Hantzsch ; M. D. de Fr. lxxviii, 6. Loc. 8. Rare.

S. BACULUS Greg. ; V. H. Syn. xlii, 9. Loc. 39. Rare ; occurs in the Carse clay.

THALASSIOTHRIX Cl. & Grun.

T. (THALASSIONEMA Grun.) NITZSCHIOIDES Grun. ; M. D. de Fr. lxxxi, 17, 18. Loc. 81. In all tow-nettings of the Tay.

ASTERIONELLA Hass.

A. FORMOSA Hass. ; V. H. Syn. li, 19. Loc. 18, 73, 81. Occurs in fresh- and salt-water plankton, the marine form being known as var. *Bleakelyi* W. Sm.

A. FORMOSA v. GRACILLIMA Grun. ; V. H. Syn. li, 22. Loc. 18. Occurs with the type.

ASTERIONELLA FORMOSA V. SUBTILIS Grun.; V. H. Syn. li, 21. Loc. 61, 76. Not uncommon.

A. JAPONICA Cl. ; Gran. Nord. Plank. 118, fig. 160. Loc. 81. In tow-nettings of the Tay.

Family XII. FRAGILARIEAE.

FRAGILARIA Lyngb.

a. STAUROSIRA.

F. CAPUCINA Desm. ; V. H. Syn. xlv, 2. Loc. 3, 7, 11, 13, 23, 50, 59, 63, 65, 80. Fairly abundant. This typically freshwater species is occasionally found in brackish and even salt water.

F. CAPUCINA V. MESOLEPTA (Rabh.) V. H. ; V. H. Syn. xlv, 3. Loc. 3, 6, 11, 43, 50, 52, 53, 79. Fairly abundant.

F. CAPUCINA V. LANCEOLATA Grun. ; V. H. Syn. xlv, 5. Loc. 6, 63. Not abundant.

F. INTERMEDIA Grun. ; V. H. Syn. xlv, 11. Loc. 3, 43, 52, 61, 74, 78. Fairly abundant.

F. MUTABILIS (W. Sm.) Grun. ; V. H. Syn. xlv, 12. Loc. 2, 4, 6, 7, 13, 44, 53, 55, 56, 61, 65, 68, 70. General, and frequently abundant. Very variable.

F. CONSTRUENS (Ehb.) V. H. f. GENUINA ; V. H. Syn. xlv, 26 *c*, *d*, 27. Loc. 6, 14, 20, 37, 44, 55, 62. Not common.

F. CONSTRUENS V. VENTER V. H. ; V. H. Syn. xlv, 26 *a*, *b*. Loc. 14, 56, 59, 61, 69, 78. In boggy pools. Most abundant on the Sidlaws.

F. CONSTRUENS V. BINODIS Grun. ; V. H. Syn. xlv, 24, 25. Loc. 20, 30, 65. Somewhat rare.

F. HARRISONII (W. Sm.) Grun. ; V. H. Syn. xlv, 28. Loc. 7, 51, 52, 53, 63, 65, 71, 78. Most abundant on the Sidlaws.

F. CROTONENSIS Kitton ; A. S. Atl. ccxcix, 1-8. Loc. 42, 61, 78. A plankton form in lochs and reservoirs. Fairly abundant at the Monikie reservoirs.

F. PARASITICA (W. Sm.) Grun. ; V. H. Syn. xlv, 30. Loc. 7, 14, 22, 43, 53, 55, 65, 68, 78, 79. Epiphytic on larger diatoms, such as *Nitzschia sigmoidea*, *Cymatopleura solea*, and *Surirella* sp.

F. BREVISTRIATA Grun. v. TURGIDA var. nov. (Text-fig. 36.) Loc. 65. Not abundant. L. 10–15 μ, b. 5–7 μ. [See Appendix p. 307.]

b. FRAGILARIA.

F. VIRESCENS Ralfs ; V. H. Syn. xliv, 1. Loc. 2, 3, 45, 49, 53, 55, 60, 64, 65, 66, 70. Most abundant on the Sidlaws.

F. VIRESCENS V. EXIGUA Grun. ; V. H. Syn. xliv, 2, 3. Loc. 6, 55. Not abundant.

F. UNDATA W. Sm. ; V. H. Syn. xliv, 9. Loc. 14. Not abundant.

F. STRIATA Lyngb. ; V. H. Syn. xliv, 12. Loc. 80. Not abundant. The valves are only slightly silicified.

GRUNOWIELLA V. H.

G. MARINA Greg. ; M. D. de Fr. lxxxiii, 4. Loc. 80. Rare.

G. PARVA Grun. ; M. D. de Fr. lxxxiii, 5. Loc. 80. Not abundant.

OPEPHORA P. Petit.

O. PACIFICA Grun. ; M. D. de Fr. lxxxiii, 3. Loc. 8, 26. Not abundant.

Family XIII. RHAPHONEIDAE.

RHAPHONEIS Ehb.

R. AMPHICEROS Ehb. ; M. D. de Fr. lxxxiii, 15a. Loc. 8, 81. Fairly abundant.

R. AMPHICEROS V. RHOMBICA Grun. ; V. H. Syn. xxxvi, 20, 21. Loc. 8, 10, 26, 27, 39, 73, 80. General in the Tay.

R. BELGICA Grun. ; M. D. de Fr. lxxxiii, 24, 26. Loc. 8, 39. Not abundant.

R. BELGICA V. INTERMEDIA Grun. ; V. H. Syn. xxxvi, 30. Loc. 27, 80. Somewhat rare.

R. SURIRELLA (Ehb.) Grun. ; M. D. de Fr. lxxxiii, 27–29. Loc. 8, 10, 27, 38, 73. Not abundant.

R. SURIRELLA V. AUSTRALIS Grun. ; V. H. Syn. xxxvi, 27b. Loc. 39. Rare.

R. NITIDA Greg. ; M. D. de Fr. lxxxiii, 31–33. Loc. 26. Rare. Only the small form known as R. liburnica Grun. occurs here.

TRACHYSPHAENIA Petit.

T. AUSTRALIS Petit ; M. D. de Fr. lxxxiii, 35. Loc. 27, 80. Somewhat rare.

Family XIV. PLAGIOGRAMMEAE.

DIMEREGRAMMA Ralfs.

D. NANUM Greg. ; M. D. de Fr. lxxxii, 15. Loc. 8. Rare.

PLAGIOGRAMMA Grev.

P. GREGORYANUM Grev. ; M. D. de Fr. lxxxii, 7. Loc. 8, 10. Rare.

Tribe 6. DIATOMEAE TABELLARIOIDAE.

Family XV. ODONTIDEAE.

DIATOMA de Candolle.

D. VULGARE Bory ; V. H. Syn. 1, 1–6. Loc. 20, 23, 25, 48, 53, 54, 61, 63, 71, 75. General, and frequently abundant.

D. VULGARE v. EHRENBERGII Grun. ; A. S. Atl. cclxviii, 26–32, 34, 36. Loc. 78. Abundant at the Monikie reservoirs.

D. ELONGATUM Ag. ; A. S. Atl. cclxviii, 37–39, 50 etc. Loc. 3, 6, 11, 26, 45, 56, 59, 61, 62, 63, 65, 78. General, and frequently abundant.

D. ELONGATUM v. HYBRIDA Grun. ; A. S. Atl. cclxviii, 54–57. Loc. 11. Occurring sparingly with the type.

D. ELONGATUM v. TENUIS Kütz. ; A. S. Atl. cclxviii, 62–67 etc. Loc. 26, 44. Fairly abundant.

D. HIEMALE Heib. ; V. H. Syn. li, 1, 2. Loc. 45, 46, 49, 51, 64, 65, 68, 69, 70, 72. A northern form, which reaches its maximum development during January and February. Frequently very abundant on the surface of rocks in quarries with a northern aspect. Auxospores (not previously found in this genus) produced sparingly towards the end of the period of maximum development.

D. HIEMALE v. MESODON (Kütz.) V. H. ; V. H. Syn. li, 3, 4. Loc. 26, 45, 47, 48, 64, 72, 78. Abundant.

D. ANCEPS Grun. ; V. H. Syn. li, 5–8. Loc. 26, 69. Not abundant.

MERIDION Ag.

M. CIRCULARE Ag. ; V. H. Syn. li, 10–12. Loc. 7, 12, 24, 25, 36, 37, 41, 48, 51, 54, 56, 57, 59, 63, 65, 68, 74, 76, 77, 81. Common in stagnant water, in ditches, and pools. Occurs in 28 per cent. of the freshwater collections, sometimes almost pure.

M. CIRCULARE v. CONSTRICTUM Ralfs ; V. H. Syn. li, 14, 15. Loc. 8, 32, 51, 66, 67, 70. Not so common as the type. The ' forme intermediaire ' of van Heurck occurs in loc. 11, 45.

Family XVI. LICMOPHOREAE.

LICMOPHORA Ag.

L. GRACILIS Ehb. v. ANGLICA Kütz. ; V. H. Syn. xlvi, 14. Loc. 18. Abundant.

L. DALMATICA Kütz. ; V. H. Syn. xlvii, 7. Loc. 18, 80. Fairly abundant. Accompanied by the forma *brevis* V. H.

L. HYALINA Kütz. ; V. H. Syn. xlviii, 6, 7. Loc. 73, 80. Fairly abundant.

L. COMMUNIS (Heib.) Grun. ; V. H. Syn. xlviii, 8, 9. Loc. 18, 80. Not uncommon.

L. PARADOXA (Lyngb.) Ag. ; V. H. Syn. xlviii, 10–12. Loc. 73, 80. Fairly abundant.

Family XVII. **TABELLARIEAE.**

GRAMMATOPHORA Ehb.

G. MARINA Kütz.; M. D. de Fr. lxxxvii, 6, 8. Loc. 8, 10, 18, 80. Fairly abundant. Includes *G. oceanica* Ehb.

G. SERPENTINA Ehb. ; M. D. de Fr. lxxxviii, 1–3, 5. Loc. 39, 80, 81. Fairly abundant.

RHABDONEMA Kütz.

R. ADRIATICUM Kütz. ; M. D. de Fr. lxxxiv, 7–11. Loc. 39. Not abundant.

R. ARCUATUM (Lyngb.) Kütz. ; M. D. de Fr. lxxxiv, 12–14. Loc. 8, 18, 39, 80, 81. Common in the Tay.

R. MINUTUM Kütz.; M. D. de Fr. lxxxiv, 5, 6. Loc. 8, 18, 22, 39, 80. Usually occurs with the above.

STRIATELLA Agardh.

S. UNIPUNCTATA Ag. ; M. D. de Fr. lxxxix, 1. Loc. 26, 73. Not uncommon.

CYCLOPHORA Castr.

C. TENUIS Castr. ; M. D. de Fr. i, 27, 32. Loc. 81. Rare. Found only in one tow-netting of the Tay.

TABELLARIA Kütz.

T. FLOCCULOSA (Roth.) Kütz. ; V. H. Syn. lii, 10–12. Loc. 2, 5, 6, 14, 42, 56, 59, 61, 64, 65, 66, 70, 80. General and frequently abundant in the plankton of locks and reservoirs.

T. FENESTRATA (Lyngb.) Kütz. ; A. S. Atl. cclxix, 11–13. Loc. 1, 2, 6, 14, 42, 64, 66, 81. Fairly abundant.

T. FENESTRATA V. ASTERIONELLOIDES Grun. ; V. H. Syn. lii, 9. Loc. 81. Not abundant.

TETRACYCLUS Ralfs.

T. RUPESTRIS (Braun) Grun. ; V. H. Syn lii 13, 14. Loc. 26. Rare.

Order II. CENTRICAE.

Tribe 7. DIATOMEAE BIDDULPHIOIDAE.

Family XVIII. BIDDULPHIEAE.

ISTHMIA Ag.

1. ENERVIS Ehb.; M. D. de Fr. xcii. Loc. 80. Rare, and usually only broken specimens found; so that it is likely that this species does not flourish in the Tay, although it is quite common at Arbroath.

ODONTELLA (Ag.) Grun.

O. (BIDDULPHIA) ROPERIANA Grev.; M. D. de Fr. xcviii, 1. Loc. 8. Very rare.

O. (BIDDULPHIA) OBTUSA Kütz.; M. D. de Fr. xcviii, 2. Loc. 80. Not uncommon.

O. (BIDDULPHIA) AURITA Ag.; M. D. de Fr. xcviii, 3–6. Loc. 8, 26, 27, 73, 80, 81. The most abundant species of this genus in the Tay.

O. (BIDDULPHIA) GRANULATA Roper; M. D. de Fr. xcvii, 6. Loc. 8, 80, 81. Fairly abundant.

O. (BIDDULPHIA) MOBILIENSIS (Bail.) Grun.; M. D. de Fr. xcvii, 1–5. Loc. 80–81. Not uncommon.

TRICERATIUM Ehb.

T. (AMPHITETRAS) ANTEDILUVIANA Ehb.; M. D. de Fr. cii, 1–4. Loc. 80. Rare.

T. FAVUS Ehb.; M. D. de Fr. xcix, 1–3. Loc. 80. Very rare.

CERATAULINA H. Per.

C. BERGONII H. Per.; M. D. de Fr. cvi, 6, 7. Loc. 81. Occurs in tow-nettings of the Tay.

Family XIX. LITHODESMIEAE.

DITYLIUM Bail.

D. BRIGHTWELLII (West) Grun.; M. D. de Fr. xcvi, 6–11. Loc. 81. In tow-nettings of the Tay.

Tribe 8. DIATOMEAE DISCOIDAE.

Family XX. HELIOPELTEAE.

ACTINOPTYCHUS Ehb.

A. UNDULATUS (Ehb.) Ralfs. ; M. D. de Fr. cxi, 1. Loc. 8, 9, 10, 18, 26, 27, 29, 37, 38, 39, 73, 80, 81. The most abundant centric diatom in the Tay. Very variable.

Family XXI. EUPODISCEAE.

EUPODISCUS Rattr.

E. ARGUS Ehb. ; M. D. de Fr. cxii, 3. Loc. 8, 80, 81. Rare.

ROPERIA Grun.

R. TESSELATA (Rop.) Grun. ; M. D. de Fr. cxii, 6. Loc. 8, 80. Rare.

Family XXII. COSCINODISCEAE.

ACTINOCYCLUS Ehb.

A. EHRENBERGII Ralfs ; M. D. de Fr. cxiv, 1, 2. Loc. 80. Not abundant.

A. RALFSII Sm. ; M. D. de Fr. cxiii, 1–6. Loc. 80. Not abundant. Peragallo considers that these two species are not really distinct, and are connected by a number of intermediate forms, of which one is *A. sparsus* Greg. I have found such a closely-related series of forms at Carnoustie.

A. CRASSUS Sm. ; M. D. de Fr. cxiv, 3, 4. Loc. 8, 80. Not abundant.

A. SUBTILIS Greg. ; M. D. de Fr. cxiv, 5, 6. Loc. 80. Not abundant.

A. ROPERII Breb. ; M. D. de Fr. cxiv, 9, 10. Loc. 80. Not abundant.

COSCINODISCUS Ehb.

C. KUETZINGII A. S. ; M. D. de Fr. cxv, 2. Loc. 27, 39, 80. Occurs sparingly at Port Allen and Carnoustie. Rare in the Carse clay.

C. SUBTILIS Ehb. ; M. D. de Fr. cxv, 4. Loc. 27, 80. Fairly abundant.

C. SUBTILIS Ehb. v. NORMANII V. H. ; M. D. de Fr. cxv, 1. Loc. 80. Fairly abundant. According to Mann the only difference between *C. subtilis* Ehb. and *Actinocyclus subtilis* Ralfs is that the former has no pseudo-nodule.

C. CURVATULUS Grun. ; M. D. de Fr. cxv, 7. Loc. 8, 81. Not abundant. In tow-nettings of the Tay. The curvature of the fasciculi is frequently very slight. Differs from *Actinocyclus curvatulus* Jan. solely in the absence of the pseudo-nodule.

COSCINODISCUS CONCINNUS Sm. ; M. D. de Fr. cxv, 12. Loc. 81. In tow-nettings of the Tay.

C. EXCENTRICUS Ehb. ; M. D. de Fr. cxvi, 3. Loc. 8, 27, 73, 80, 81. Abundant.

C. EXCENTRICUS v. MINOR Per. ; M. D. Fr. cxvi, 4. Loc. 26, 39, 80. Less common than the type.

C. LINEATUS Ehb. ; M. D. de Fr. cxvi, 7. Loc. 8, 28, 80, 81. Occurs in the tow-nettings of the Tay. Not uncommon.

C. LINEATUS f. MINOR ; M. D. de Fr. cxvi, 9. Loc. 27. Not abundant.

C. ANGUSTE-LINEATUS A. S. ; A. S. Atl. lix, 34 ; Gran. Nord. Plank. f. 30 b. Loc. 80. Rare.

C. MARGINATUS Ehb. ; M. D. de Fr. cxvii, 6. Loc. 8, 27, 39, 80, 81. One of the commonest species, and found in all tow-nettings of the Tay.

C. OCULUS-IRIDIS Ehb. ; M. D. de Fr. cxviii, 2. Loc. 80, 81. Not abundant.

C. CENTRALIS Ehb. ; M. D. de Fr. cxviii, 1. Loc. 80, 81. Not abundant.

C. ASTEROMPHALUS Ehb. ; A. S. Atl. cxiii, 23 ; V. H. Syn. cxxx, 1, 2, 5, 6. Loc. 80, 81. Not abundant.

C. ASTEROMPHALUS v. HYBRIDA Grun. ; A. S. Atl. cxiii, 22. Loc. 80. Rare.

C. RADIATUS Ehb. ; M. D. de Fr. cxvii, 3. Loc. 8, 27, 39, 81. The most abundant species of this genus. Occurs in all tow-nettings of the Tay.

C. RADIATUS v. MEDIUS Grun. ; A .S. Atl. cxiii, 21. Loc. 80. Rare.

C. RADIATUS v. MINOR A. S. ; M. D. de Fr. cxvii, 4, 5. Occurs with the type.

C. WOODWARDII Eulen. ; A. S. Atl. lx, 8, lxi, 3. Loc. 80. Rather uncommon. =C. apiculatum v. Woodwardii Rattr. After carefully examining this species (April 1925) I made the following notes :—' I think Rattray errs in making this a variety of C. apiculatus Ehb. as it is quite distinct from that species. It seems more closely allied to, but yet distinct from, C. hetero-porus Ehb. (but with a more radial arrangement), C. crassus Bail., C. gigas v. punctiformis Rattr., and C. argus Ehb.' Some time after writing the above I obtained a copy of Mann's Diat. Albatross, 1888/1904, and found that Mann had previously arrived at the same conclusion (l.c. p. 260).

C. NITIDUS Greg. ; M. D. de Fr. cxvii, 12. Loc. 8, 27, 80. Not abundant.

Note.—C. concavus Greg. has been placed in the genus Endictya Ehb.

CYCLOTELLA Kütz.

C. STRIATA (Kütz.) Grun. ; V. H. Syn. xcii, 6–10. Loc. 8, 26, 27, 29. Common but not abundant in brackish and salt water.

C. STRIATA V. BIPUNCTATA Fricke ; A. S. Atl. ccxxiii, 15–19. Loc. 26. Rare.

C. STRIATA V. AMBIGUA Cl. & Grun. ; A. S. Atl. ccxxiii, 20. Loc. 28. Rare.

C. COMTA (Ehb.) Kütz. ; V. H. Syn. xcii, 16–22. Loc. 17, 18, 26, 45, 60, 61, 65, 78. The commonest species of this genus in the district.

C. COMTA V. RADIOSA Grun. ; V. H. Syn. xcii, 3 ; xciii, 1–9. Loc. 14, 62, 63, 64. Not so common as the type.

C. SEVILLEANA Deby ; A. S. Atl. ccxxii, 33, 34. Loc. 26. Rare.

C. SEXNOTATA Deby ; A. S. Atl. ccxxii, 35, 36. Loc. 5, 14. Rare. De Toni includes the last two species in ' Species mihi tantum nominae notae aut perdubiae '. Pelletan ('Les Diatomées ', p. 206) gives descriptions of *C. Sevilleana* and *C. sexpuncta* (*sexnotata*), and remarks that these two forms, as far as known, have only been found in the fossil deposit at Seville. The names given in A. S. Atl. ccxxii are corrected in ccxxv. *C. sevilleana* occurs sparingly in the canalised stream near the Brick and Tile Works, Glencarse ; *C. sexnotata* occurs sparingly in Tentsmuir and Forgan Bog ; in both localities only the form with eight puncta was found (text-fig. 37). The occurrence of these two species, previously only found as fossils in the Seville deposit, is noteworthy.

C. KUETZINGIANA Chauvin ; V. H. Syn. xciv, 1, 4, 6. Loc. 6. Not abundant.

C. MENEGHINIANA Kütz. ; V. H. Syn. xciv, 11, 13. Loc. 26. Not abundant.

C. MENEGHINIANA V. RECTANGULATA Grun. ; V. H. Syn. xciv, 17, 19. Loc. 19, 26, 56. Commoner than the type.

C. MENEGHINIANA V. PUMILA Grun. ; V. H. Syn. xciv, 16. Loc. 19. Rare.

C. MENEGHINIANA V. STIGMATA, var. nov. (Text-fig. 38.) Loc. 6. Somewhat rare. Size 15 μ ; central area 5 μ. Central area with a peripheral ring of usually equidistant isolated puncta, most frequently eight, and with irregularly scattered central puncta. [See Appendix, p. 307.]

C. OPERCULATA Kütz. ; V. H. Syn. xciii, 23–24. Loc. 4, 52. Not common.

Family XXIII. **XANTHIOPYXIDEAE.**

STEPHANODISCUS Ehb.

S. HANTZSCHII Grun. ; V. H. Syn. xcv, 10. Loc. 27. Rare.

S. ASTREA (Ehb.) Grun. ; V. H. Syn. xcv, 5. Loc. 27. Rare.

THALASSIOSIRA Cl.

T. NORDENSKIOLDII Cl. ; M. D. de Fr. cxx, 7. Loc. 39, 81. Occurs frequently in tow-nettings of the Tay.

THALASSIOSIRA NORDENSKIOLDII V. GRAVIDA Cl.; M. D. de Fr. cxx, 8. Loc. 81. Not uncommon.

T. DECIPIENS (Grun.) Jorg.; Nord. Plank. Gran. f. 10. Loc. 8, 10, 26, 29, 73, 80. Common in the Tay.

T. DECIPIENS V. CONDENSATA Cl.; Nord. Plank. Gran. f. 15. Loc. 81. Rare.

COSCINOSIRA Gran.

C. POLYCHORDA Gran.; Nord. Plank. Gran. f. 17. Loc. 81. Rare.

SKELETONEMA Grev.

S. COSTATUM (Grev.) Cl.; M. D. de Fr. cxxi, 5. Loc. 80, 81. Common in the plankton of the Tay.

STEPHANOPTYXIS Ehb.

S. TURRIS Grev.; M. D. de Fr. cxix, 17. Loc. 80, 81. Not abundant.

Family XXIV. **MELOSIREAE.**

ENDICTYA Ag.

E. OCEANICA Ehb.; M. D. de Fr. cxix, 1. Loc. 8, 26. Not abundant. This is the *Coscinodiscus concavus* of Gregory. It is still included by Mann in *Coscinodiscus*.

HYALODISCUS Ehb.

H. STELLIGER Bail.; M. D. de Fr. cxix, 5. Loc. 8, 26, 37, 39, 80, 81. Common in the Carse clay and in the Tay.

H. RADIATUS O'Meara; M. D. de Fr. cxix, 6. Loc. 39. Rare.

H. SUBTILIS Bail.; M. D. de Fr. cxix, 7. Loc. 80. Not abundant.

H. SUBTILIS V. SCOTICA Grun.; M. D. de Fr. cxix, 8. Loc. 10, 27, 80. Not abundant.

DRURIDGEA Donk.

D. GEMINATA Donk.; M. D. de Fr. cxx, 16. Loc. 9, 19, 27. Rare. Found on sands at Tayport and on the surface of mud at Port Allen.

MELOSIRA Ag.

To include the forms found in the area I have adopted the following modified classification :—

1. Valves simply punctate .... **Melosira.**
    Section A. *Eumelosira* Schutt.
       „   B. *Lysigonium* Link.
       „   C. *Gaillionella* Bory.
2. Valves punctate and areolate ...., **Paralia.**

Melosira.

Eumelosira.

M. DISTANS Kütz. ; V. H. Syn. lxxxvi, 21–23.   Loc. 14, 70.   Rare at Forgan Bog; abundant in *Sphagnum* pools.   Craigowl, Sidlaws.   This species and its varieties are considered to be sub-alpine forms.

M. DISTANS v. NIVALIS W. Sm. ; V. H. Syn. lxxxvi, 25–27.   Loc. 70.   Not abundant, occurring with the type.

M. DISTANS v. ALPIGENA Grun. ; V. H. Syn. lxxxvi, 28, 29.   Loc. 67.   Rare, in boggy pools.

M. LYRATA Kütz. ; V. H. Syn. lxxxvii, 1, 2.   Loc. 67.   Fairly abundant. A typical sub-alpine species.

M. LYRATA v. LACUSTRIS Grun. ; V. H. Syn. lxxxvii, 3.   Loc. 67.   More abundant than the type.

M. LYRATA f. TENUIORES Grun. ; V. H. Syn. lxxxvii, 4, 5.   Loc. 67.   Not uncommon.

M. GRANULATA (Ehb.) Ralfs ; V. H. Syn. lxxxvii, 10–12.   Loc. 8, 14, 81. Not abundant.

M. GRANULATA v. AUSTRALIENSIS Grun. ; V. H. Syn. lxxxvii, 13–16.   Loc. 55. Rare.

M. CRENULATA (Ehb.) Kütz. ; V. H. Syn. lxxxviii, 3–5.   Loc. 51, 66, 67, 68, 73, 80.   Variable and usually accompanied by its varieties.

M. CRENULATA v. TENUIS (Kütz.) Grun. ; V. H. Syn. lxxxviii, 9–10.   Loc. 42, 66.   Fairly abundant.

M. CRENULATA v. TENUISSIMA Grun. ; V. H. Syn. lxxxviii, 11.   Loc. 42, 80.   Not abundant.

M. CRENULATA v. LINEOLATA Grun. ; V. H. Syn. lxxxviii, 1–2.   Loc. 26, 66, 67.   Not abundant.

M. CRENULATA v. LEVIS Grun. ; V. H. Syn. lxxxviii, 19.   Loc. 66.   Rare.

M. CRENULATA v. AMBIGUA Grun. ; V. H. Syn. lxxxviii, 12–15.   Loc. 55, 59, 67.   Not abundant.

M. ARENARIA Moore ; V. H. Syn. xc, 1–3.   Loc. 39, 53, 71.   Not abundant. Occurs sparingly in the Carse clay.

Lysigonium.

M. BORRERI Grev. ; V. H. Syn. lxxxv, 5–8.   Loc. 18, 81.   Not abundant.

M. VARIANS Ag. ; V. H. Syn. lxxxv, 11.   Loc. 7, 11, 23, 24, 30, 35, 38, 51, 71, 78.   One of the most abundant of centric diatoms ; occurs frequently in ponds, ditches, and slow-running water.

M. JURGENSII Ag. ; V. H. Syn. lxxxvi, 1–3, 5.   Loc. 18, 38.   Fairly abundant.

Gaillionella.

M. NUMMULOIDES (Bory) Ag.; V. H. Syn. lxxv, 1, 2. Loc. 22, 38, 73.
Not uncommon.

M. WESTII W. Sm.; V. H. Syn. xci, 11, 12. Loc. 10, 80. Not abundant.

Paralia.

M. SULCATA (Ehb.) Kütz.; M. D. de Fr. cxix, 11. Loc. 10, 26, 28, 29, 30,
39, 80, 81. One of the commonest diatoms in the Tay. Variable and usually
mixed with its varieties.

M. SULCATA f. RADIATA Grun.; M. D. de Fr. cxix, 12. Loc. 26, 29, 30,
80, 81. Abundant.

M. SULCATA f. CORONATA (Ehb.) Grun.; M. D. de Fr. cxix, 13. Loc. 26,
30, 80. Not abundant.

M. SULCATA v. BISERIATA Grun.; M. D. de Fr. cxix, 14. Loc. 29, 39, 80.
Somewhat rare.

Tribe 9. DIATOMEAE SOLENIOIDAE.

Family XXV. **DACTYLIOSOLENIAE.**

LEPTOCYLINDRUS Cl.

L. DANICUS Cl.; M. D. de Fr. cxxii, 4. Loc. 81. Not abundant; in tow-
nettings of the Tay.

LAUDERIA Cl.

L. BOREALIS Gran.; M. D. de Fr. cxxi, 2. Loc. 81. Occurs sparingly
in tow-nettings of the Tay.

Family XXVI. **RHIZOSOLENIAE.**

STREPTOTHECA Shrubs.

S. THAMENSIS Shrubs.; M. D. de Fr. cxxi, 10. Loc. 81. Occurs sparingly
in tow-nettings of the Tay.

GUINARDIA Cl.

G. FLACCIDA (Castr.) H. Per.; M. D. de Fr. cxxii, 1-3. Loc. 81. Occurs
in tow-nettings of the Tay.

RHIZOSOLENIA (Ehb.) Brightw.
A. Affines.

R. DELICATULA Cl.; M. D. de Fr. cxxiv, 6. Loc. 81. Occurs in tow-nettings
of the Tay.

R. STOLTERFOTHII H. Per. ; M. D. de Fr. cxxii, 7.   Loc. 81.   Not abundant.

R. FRAGILISSIMA Bergon ; M. D. de Fr. cxxi, 6, 7, cxxiv, A, f. 8.   Loc. 81. Rare.   Found in only one tow-netting.

R. FAEROEENSIS Ostenf. ;   Nord. Plank. Gran. f. 53. Loc. 81. Not abundant.

<h2 style="text-align:center">B. Genuinae.</h2>

R. STYLIFORMIS Brightw. ; M. D. de Fr. cxxiv, 2, 6.   Loc. 81.   Not abundant.

R. SETIGERA Brightw. ; M. D. de Fr. cxxiv, 11, 12, 14.   Loc. 81.   Fairly abundant.

R. SEMISPINA Hensen. ; M. D. de Fr. cxxiv, 13, 15.   Loc. 81.   The most abundant species of *Rhizosolenia* in the Tay.   This is considered to be one of the forms of the dimorphic *R. hebetata* Bail.

R. SHRUBSOLEI Cl. ; M. D. de Fr. cxxiv, A, 5.   Loc. 81.   Not abundant.

Tribe 10. DIATOMEAE   CHAETOCEROIDAE.

Family XXVII. CHAETOCEREAE.

CHAETOCEROS Ehb.

The following species occur in tow-nettings of the Tay (loc. 81) :

Section Robusta.

C. DANICUM Cl. ; M. D. de Fr. cxxvii, 1.

C. BOREALE Bail. ; M. D. de Fr. cxxvii, 2.

C. DENSUM Cl. ; M. D. de Fr. cxxvii, 4.

Section Affinia.

C. CURVISETUM Cl. ; M. D. de Fr. cxxix. 4.

C. SIMILE C. ; M. D. de Fr. cxxxii, 4.

C. SKELETON Cl. ; M. D. de Fr. cxxxiv, 9.   Loc. 73.   Found in rich diatomaceous material scraped from floating logs in Earl Grey Dock.   Lat. 56° 27'. According to Cleve ('Phytoplank. of the Atlantic Ocean') this species occurs in the warm parts of the Atlantic and as far north as 49° 53'.   Gran (Nord. Plank. p. 67) says :—'Tropical and sub-tropical Atlantic, northern limits 65° N. Br.'

Section **Genuina.**

C. LACINIOSUS Schutt & spores ; M. D. de Fr. cxxxii, 6.

C. DECIPIENS Cl. ; M. D. de Fr. cxxxi, 4–8.

C. PARADOXA Cl. & spores ; M. D. de Fr. cxxxii, 1, 2. =C. DIADEMA Gran.

C. TERES Cl & spores ; M. D. de Fr. cxxxiv, 1.

Section **Setosa.**

C. DEBILE Cl. ; M. D. de Fr. cxxxiv, 7.

C. SOCIALE Lauder ; M. D. de Fr. cxxxii, 1–3.

C. CONSTRICTUM Gran. ; M. D. de Fr. cxxxiv, 5.

C. SCOLOPENDRA Cl. ; Gran. Nord. Plank. p. 93, f. 119.

APPENDIX :

DESCRIPTIONS OF NEW SPECIES, VARIETIES, AND FORMS.

ACHNANTHES SIMILIS, sp. n. Valvis elliptico-lanceolatis, apicibus sub-acutis, 20–30μ longis, 7–10μ largis ; valva superiori areola anguste lanceolata ; striis 14 in 10μ, medio parallelis, ad apices radiatis ; valva inferiori areola axiali indistincta areolaque centrali magna et orbiculari ; striis 14 in 10μ plerumque radiatis. (P. 234.)

MASTOGLOIA CANALICULA, sp. n. Valvis linearibus vel lineari-lanceolatis, 40–45μ longis, 8–9μ largis, apicibus late capitatis ; frustulis facie connectivali angustis linearibus, marginalibus parvis et orbiculatis circa 3 in 10μ ; rhaphe in utroque latere loculo vel canali donata ; striis parallelis circa 28 in 10μ ; area axiali angustissima, area centrali parva et orbiculata. (P. 238.)

CALONEIS SILICULA v. JENISSEYENSIS Grun. f. PARVA, f. nov. Quam varie-tatem minor. (P. 239.)

CALONEIS SUBLINEARIS, sp. n. Valvis late linearibus, 30–40 μ longis, 10–13 μ largis, apicibus subcuneatis ; area axiali medio in aream orbicularem abrupte dilatata ; rhaphe recta, fissuris hamatis terminalibus et poris centra-libus parvis, nonnihili distantibus ; striis parallelis, in apicibus leniter radiatis, leviter granularibus, sed non distincte punctatis ; lineis longitudinalibus infra marginem. (P. 240.)

NEIDIUM CAPITATUM, sp. n. Valvis linearibus 50–60μ longis, 12–15μ largis, apicibus capitatis ; striis delicatis. (P. 242.)

NEIDIUM IRIDIS v. BRYOPHILUM, var. nov. Valvis linearibus 40–50μ longis, 13–17μ largis, marginibus subparallelis ad apices rotundatos contractis ; striis 17–18, punctis 17 in 10μ. (P. 242.)

NEIDIUM IRIDIS V. ROBUSTUM, var. nov. Valvis lineari-ellipticis, 90–100 μ longis, 23–36 μ largis, apicibus subcuneatis ; striis 12 in 10 μ, obliquis, robustis ; punctis 12 in 10 μ. (P. 242.)

NEIDIUM AMPHIGOMPHUS V. INTERMEDIUM, var. nov. Valvis late linearibus, 80–95 μ longis, 20–25 μ largis, apicibus subcuneatis ; striis 15, punctis 16 in 10 μ. (P. 242.)

DIPLONEIS OVALIS V. OBLONGELLA f. GIBBOSA, f. nov. Valvis medio leniter gibbosis. (P. 243.)

DIPLONEIS NITESCENS Greg. v. CANDIDA, var. nov. Valvis ellipticis nonnihili subrectangularibus, 50–60 μ longis, 28–32 μ largis ; nodula centrali parva, rectangulari ; cornubus angustissimis, indistinctis ; sulcis latis, marginibus eorum aream lanceolatum, trientem valvae, continentibus, costis 8 in 10 μ, alveolarum ordine duplici variantibus ; alveolae marginem versus separantes, 14–16 in 10 μ. (P. 244.)

NAVICULA MUTICA f. GIBBOSA, f. nov. Valvis lanceolatis medio gibbosis. (P. 245.)

NAVICULA MUTICA f. ORNATA, f. nov. Valvis elliptico-lanceolatis, medio gibbosis ; punctis 4 rhombo dispositis in area centrale, puncto singulari oppositis. (P. 245.)

NAVICULA MUTICA V. PULCHRA. Valvis linearibus, 25–30 μ longis, 8–11 μ largis, marginibus triundulatis, gibbo medio non prominente ; apicibus latis rostrato-capitatis ; striis radiatis, ad apices subparallelis, 18 in 10 μ ; valde punctatis, punctis 12 in 10 μ ; area axiali angusta sed distincta ; area centrali fascia lata transversaque, lineari sed ad marginem lente dilata, ubi sunt striae marginales brevissimae ; area puncto singulari. (P. 245.)

NAVICULA INFLATA V. ROSTRATA, var. nov. Valvis lanceolatis, 16–25 μ longis, 5–7 μ largis, apicibus rostratis ; striis medio 18, apicibus 22–24. (P. 246.)

NAVICULA RELICTA, sp. n. Valvis linearibus, 20–30 μ longis, 5–8 μ largis, ad apices rotundatos leniter contractis ; striis 20 in 10 μ radiatis, ad apices parallelis ; punctis 20 in 10 μ ; costis robustioribus quam in *N. gibbula*. (P. 248.)

STAURONEIS PARVULA V. ATTENUATA, var. nov. Valvis lineari-lanceolatis, 35–50 μ longis, 8–11 μ largis, apicibus attenuatis vel producto-rostratis et diaphragmatibus apicalibus ; striis radiatis 22 in 10 μ, stauro non amplo, marginem versus leniter attenuato. (P. 249.)

NAVICULA COCCONEIFORMIS f. PARVA, f. nov. Typo minor, 15 μ longa, 8 μ larga. (P. 250.)

NAVICULA PEREGRINA V. PRODUCTA, var. nov. Valvis lanceolatis, apicibus producto-subacutis, quam 3 μ minus latis ; striis medio 6, dein 8·5, ad apices 10 in 10 μ ; lineolis 20 in 10 μ ; area centrali transverse elliptica. (P. 252.)

NAVICULA SERPENTINA, sp. n.   Valvis late lineari-lanceolatis, 35–40μ longis, 10–12μ largis, apicibus obtusis ; area axiali mediocriter lata, lineari, ad apices angusta, medio abrupte dilatata in aream centralam magnam et sub-rhomboidalem ; rhaphe obliqua, flexuosa ; striis 14–15 in 10μ, leniter radiatis, grosse punctatis, punctis medio 12 ad apices 15 in 10μ.   (P. 255.)

ANOMOEONEIS SPHAEROPHORA V. INTERMEDIA, var. nov.   Valvis elliptico-lanceolatis, 50–70μ longis, 16–18μ largis, apicibus rostrato-capitatis ; striis 15 in 10μ ; area centrali cum areis lunatis irregularibus modo *A. sculptae* Ehb. (P. 256.)

PINNULARIA DIVERGENTISSIMA f. SUBACUTA f. nov.   A typo differt apicibus subacutis.   (P. 259.)

PINNULARIA BACILLA, sp. n.   Valvis linearibus, marginibus parallelis et apicibus rotundatis, 30–45μ longis, 6–8μ largis, costis 9 ; area axiali ab apicibus ad medium paulatim dilatante ubi latissima ;   striis intermediis brevissimis ; rhaphe filiformi simplici, poris centralibus distantibus et fissuris falciformibus terminalibus ab apicibus nonnihili distantibus ; striis fere parallelis. (P. 259.)

PINNULARIA MAJOR V. DUBIA, var. nov.   A typo differt rhaphe subcomplexa. (P. 261.)

PINNULARIA WESTII, sp. n.   Valvis linearibus, 60–120μ longis, 10–20μ largis, ad apices subcuneatis vel rotundatis leniter contractis ; area axiali triente latitudinis valvae, ad polas paulatim contracta ; area centrali fascia transversali ; rhaphe leniter undulata, obliqua sed non complici, fissuris magnis, falciformibus ; costis 7·5 in 10μ, medio subrabiatis, in apicibus leniter convergentibus.   (P. 261.)

PLEUROSIGMA DELICATULUM var. GRACILE, var. nov.   Typo minor et tenuior, 110–125μ longa, 13–16μ larga.   (P. 264.)

PLEUROSIGMA ANGULATUM V. ROBUSTUM, var. nov.   Valvis ut in typo, punctis robustioribus, 220–280μ longis, 40–50μ largis.   (P. 265.)

GYROSIGMA ACUMINATUM V. NEGLECTUM, var. nov.   A typo differt striis robustioribus.   (P. 266.)

GYROSIGMA ATTENUATUM V. GIGAS, var. nov.   Typo major et striis robusti-oribus.   (P. 266.)

GYROSIGMA DISTORTUM V. UNDULATUM, var. nov.   Valvis lineari-lanceolatis nonnihili sigmoideis, marginibus triundulatis, apicibus obtusis.   (P. 267.)

AMPHIPRORA LATA V. ANGUSTIOR, var. nov.   Frustulis siliceis, medio con-strictis, 90–110μ longis, 28–32μ largis, constrictione 23μ, apicibus rotundatis ; carina lata, linea conjunctiva arcuata ; carinae et valvae striis equidistantibus, 13 in 10μ ; carinae iis punctis parvis terminantibus ; membrana connexiva divisionibus longitudinalibus numerosis, striis transversalibus subtilissimis. (P. 268.)

AMPHIPRORA ROBUSTA, sp. n. Frustulis siliceis, valde constrictis, 85–95 μ longis, 28–32 μ largis, carinarum marginibus valde siliciferis ; linea conjunctiva arcuata ; carinarum striis robustis 8–10 in 10 μ, valvarum subtilissimis divergentibus, 29–30 in 10 μ. (P. 269.)

CYMBELLA DELICATULA V. INTERMEDIA, var. nov. Valvis angustis, linearilanceolatis, 25–35 μ longis, 5–6 μ largis, inaequilateralibus, ad apices subrostratis productis ; area axiali angustissima indistincta, area centrali parva ; rhaphe fere centrali, subarcuata ; striis medio subradiatis, ad apices parallelis. (P. 269.)

CYMBELLA SYMMETRICA, sp. n. Valvis fere aequilateralibus, sublanceolatis angustis, 35–50 μ longis, 9–12 μ largis, apicibus subacutis ; rhaphe fere recta et fere centrali ; area axiali angusta, area centrali orbiculari ; striis omnibus radiatis, subtilissime lineatis, medio 14 in 10 μ, in apicibus 16–18 in 10 μ. (P. 270.)

CYMBELLA ASPERA Ehb. v. GIGAS, var. nov. Valvis, 300–350 μ longis, 40–50 μ largis ; punctis 10 in 10 μ ; area axiali 8–9 μ larga ; area centrali 15 μ larga. (P. 272.)

AMPHORA ARENICOLA V. MINOR, var. nov. Valvis 25–30 μ longis, 12–14 μ largis ; striis 14 in 10 μ. (P. 273.)

NITZSCHIA TRYBLIONELLA V. RECTA, var. nov. Valvis linearibus, 50–60 μ longis, 8–10 μ largis, marginibus parallelis, apicibus cuneatis ; striis, et carinae punctis, 12 in 10 μ. (P. 280.)

HANTZSCHIA AMPHIOXIS V. LANCEOLATA, var. nov. Valvis sublanceolatis, 50–60 μ longis, 68 μ largis, marginis ventralis medio constrictione parva, apicibus capitatis ; carinae punctis 10–11 in 10 μ ; striis 22 in 10 μ, subtile punctatis, parallelis, in apicibus convergentibus. (P. 286.)

HANTZSCHIA RIGIDA, sp. n. Valvis fere rectis, 40–50 μ longis, 6–7 μ largis ; margine dorsali medio leniter concava, margine ventrali convexa ; apicibus rectis, productis, linearibus ; striis 16 in 10 μ, punctatis, parallelis ; carinae punctis 7 in 10 μ, elongatis, medio duobus distantioribus. (P. 286.)

FRAGILARIA BREVISTRIATA Grun. v. TURGIDA, var. nov. Valvis 10–15 μ longis, 5–7 μ largis. (P. 292.)

CYCLOTELLA MENEGHINIANA V. STIGMATA, var. nov. Valvis 15 μ diametro ; area centrali 5 μ, punctis frequenter 8, singularibus et aequidistantibus, annulo marginali dispositis ; punctis centralis sparsis. (P. 299.)

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On *Scolecopteris Oliveri.*—Part II. The vegetative organs.
By D. H. SCOTT, M.A., Ph.D., F.R.S., F.L.S., and H. S. HOLDEN, D.Sc., F.L.S.

(PLATE 27, and 11 Text-figures)

[Read 27 October 1932]

THE material upon which this study is based consists of sections of a number of rachises bearing fertile and sterile pinnules.* There is also a much flattened axis which may belong to the same plant and which is possibly a rachis of a higher order. In addition to these there are numerous sections of small leaflets of a different type which it was thought might also belong to *Scolecopteris Oliveri*, but which we now consider to have belonged to another plant. These will be described in a subsequent paper.

External morphology.

Both rachis and pinnules are small, the former having a diameter of about 1·75 mm., whilst the latter appear to have been about 6 mm. in length and to have had an average diameter of approximately 3·5 mm. They are slightly narrowed at their point of attachment to the rachis and have rounded apices. Each pinnule is united to the rachis by the whole of its base, a feature illustrated in text-fig. 1, in which the margin of the uppermost pinnule figured is shown to be continuous with the superficial tissues of the rachis. The margin of each pinnule is flexed downwards, this flexure becoming more pronounced distally, so that near the apex the edges are only separated by a narrow gap (text-figs. 3 b, 3 c). In texture the pinnules were evidently somewhat fleshy, as will be evident from a consideration of text-fig. 2, in which a transverse section of a pinnule and of the midrib and the adjacent lamina of a holly-leaf are drawn side by side at the same magnification. The venation is of the open type without anastomoses. Traversing the centre of the pinnule for the greater part of its length is a midrib from which the lateral veins are given off alternately though close together, these bifurcating near their bases (Pl. 27. fig. 7) and, in some cases at least, forking again. Towards the apex the midrib undergoes equal dichotomy and the branches also fork (Pl. 27. fig. 1). The end of each vein is expanded and modified to form a typical hydathode (Pl. 27. figs. 6 & 11–13). It will be evident that the venation is essentially

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* The slides containing material of *Scolecopteris Oliveri* which have been used in this study are nos. 148.1, 148.2, 148.2*, 148.3, 148.4, 148.5, 148.6, 148.7, and 148.8 in the possession of the senior author, nos. 148.B1, 148.B2, 148.B3, 148.B4, 148.B5, 148.B6, 148.B7 in the possession of the junior author, and nos. 1193–3, 1193–4, 1193–5 from the Collection Ch. Eug. Bertrand. With the exception of those from the Bertrand Collection, these were all cut from one block by Mr. W. Hemingway of Derby.

dichotomous in plan, sympodially developed, to use Bower's terminology, in its proximal part (1923). A restoration to scale of a single pinnule is shown in text-fig. 4.

Anatomy.

(a) *The rachis.*—The rachis is rounded as seen in transverse section with an epidermis composed of small cells. No stomata have been detected, but hairs similar in type to those borne by the pinnules (*q.v.*) have been observed in one or two instances. The vascular supply consists of an undivided U-shaped strand with the concavity adaxial (Pl. 27. figs. 3 & 4). The basal part is about three tracheids in width, but the arms are thinner (1–2 tracheids). The metaxylem tracheids are elongated scalariform elements of the usual filicinean type. The protoxylem, which is endarch and is distributed discontinuously along the concavity of the trace, consists of tracheids of small calibre with lax spiral thickening and often showing indications of disruption, though nothing in the nature of cavity parenchyma could be detected. Larger tracheids with close spiral bands occur between the smaller protoxylem tracheids and those with scalariform pitting. The phloem forms a narrow strip two or three cells in width which follows the contours of the xylem. It is not sufficiently well preserved to show the sieve-plates, but its cells are characterised by coarsely granular contents which appear to be peculiar to them. The phloem is surrounded in turn by a narrow strip of parenchyma, external to which is a well-developed, approximately cylindrical sheath of thick-walled cells enclosing the whole strand. From this a long strip of similar tissue, resembling a tongue in transverse section, and evidently acting as a supporting buttress, extends into the concavity of the vascular bundle. A similar but smaller and much less prominent ridge projects from the sheath on the adaxial side. The cells of the sheath are somewhat elongated with ends which may be either truncated or pointed (cf. Pl. 27. fig. 2). Their walls are provided with small, simple, oval pits. Between the sheath and the epidermis is a strip of parenchyma several cells in width.

(b) *The pinna trace.*—The pinna traces are C-shaped strands which are given off from the free ends of the rachis bundle. One is clearly shown, still attached but on the point of separation, on the right side of fig. 4 (Pl. 27), whilst on the left-hand side the tip of the rachis bundle is flexed, this presumably being an earlier stage in the initiation of the pinnule trace. It is also endarch, and remains of the collapsed protoxylem may often be detected lying along its adaxial concavity (Pl. 27. fig. 8). Like that of the rachis, this trace is surrounded by a sheath of thicker-walled cells which is widest abaxially and narrowest adaxially. It passes into the pinnule without division.

(c) *The pinnule.*—The epidermis of the pinnule consists of small cells with dark contents which are polygonal as seen in surface-view and which appear approximately rectangular as seen in transverse section (text-figs. 5 & 6).

The upper epidermis is devoid of stomata and of dermal appendages. Isolated

[148·2]

I.

3a.

[1193·4]

3b.

3c.

4.

[148·3]

2.

Ilex.
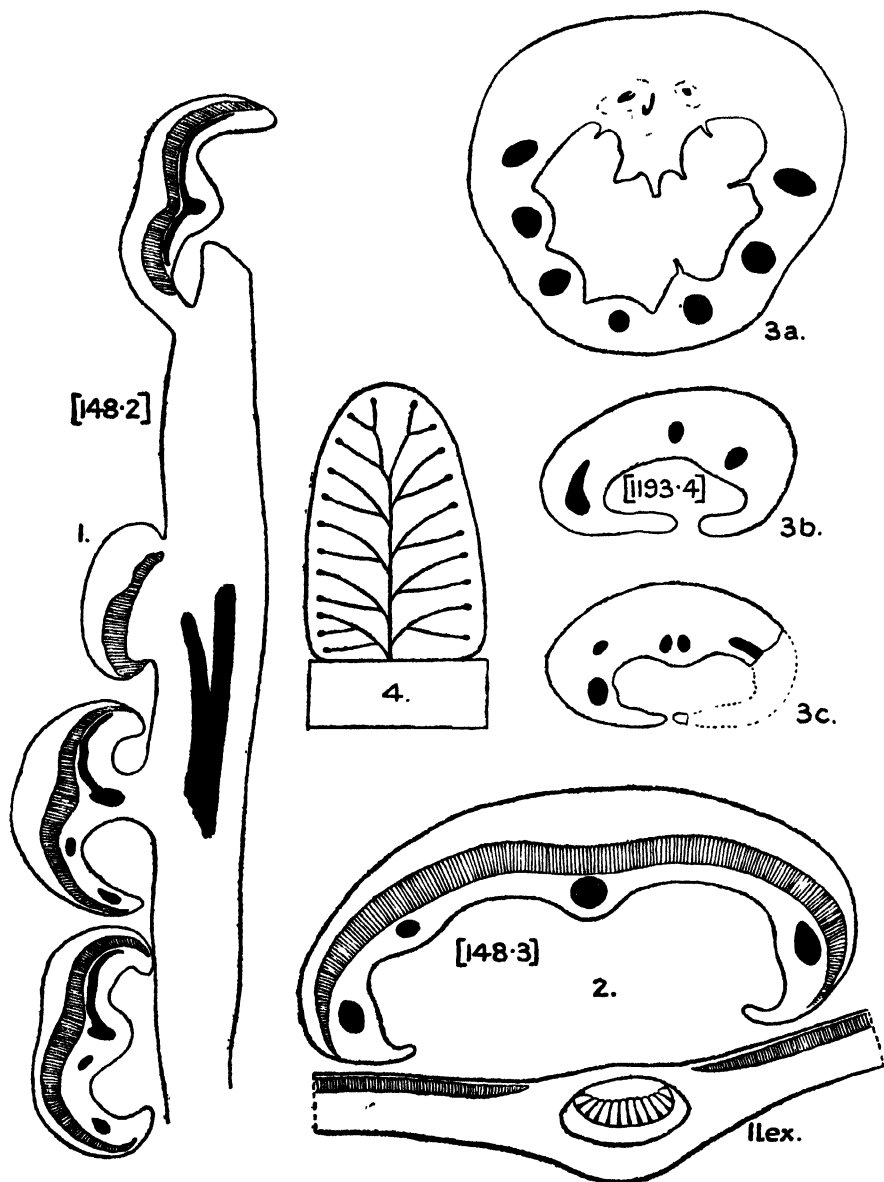
Fig. 1.—Camera-lucida outline of an oblique section of a rachis bearing four pinnules. The one nearest the top of the figure shows the attachment of the edge of the pinnule to the rachis. × 10.*

Fig. 2.—Transverse section of a pinnule to show the downward flexure of the margins and distribution of the tissues. Below it is part of a transverse section of a holly leaf at the same magnification for comparison. × 20.

Figs. 3 a, b, c.—Sections cut near the apices of pinnules; 3 a is an oblique section; 3 b and 3 c are transverse. All × 24.

Fig. 4.—Restoration of a single pinnule. × 7.

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* The figures in square brackets in these and other text-figures are those of the slides from which the drawings have been made. Fig. 3 a is [148.B1].

2 ▲ 2

cells and small groups of cells of similar character occur in the sub-epidermal region, but the bulk of the hypodermal tissue consists of large, rounded, thin-walled cells forming a layer from three to five cells in depth, though thinning out to a single cell marginally (Pl. 27. figs. 14 & 15). Exceptionally this tissue may be only one cell in thickness in the middle of the pinnule and

[148·5]   5.

[148 B5]   6.
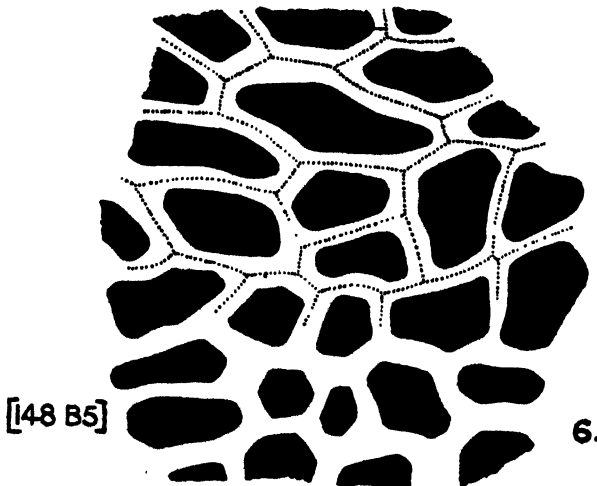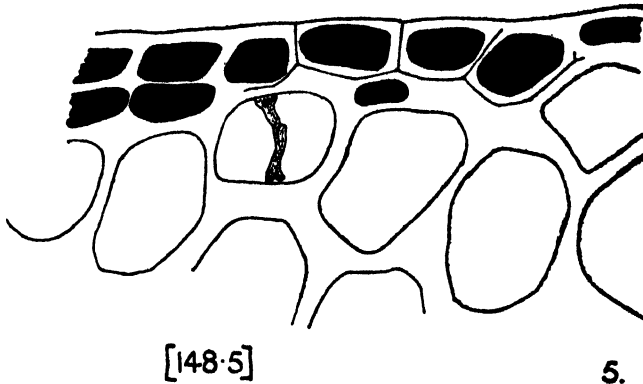
Fig. 5.—Section through the upper epidermis and subjacent aqueous tissue of a pinnule. × 333.

Fig. 6.—Surface-view of the upper epidermis of a pinnule.   × 333.

an example showing this condition on one side of the midrib is shown in Pl. 27. fig. 5. It seems reasonable to interpret this as aqueous (i.e. water-storing) tissue, as it closely resembles tissue of this nature shown in other succulent leaves. Aqueous tissue is somewhat rare in ferns, but that present in the pinnae of *Polypodium americanum* is very similar both in character

and amount. Water-storing tissue, though in this instance only one cell in thickness, is also figured by W. R. B. Oliver (1930) in *Asplenium flaccidum*. Immediately below the water-storing tissue is a zone of palisade parenchyma, one or two cells in depth, composed of very narrow elongated cells. This also thins out marginally (Pl. 27. fig. 14). Below it again is the spongy parenchyma traversed by the veins of the pinnule and consisting of loosely massed rounded cells bounded by the lower epidermis. Immediately below each vein the mesophyll is more compact and forms a projecting ridge on the lower surface (Pl. 27. fig. 7). This ridge is very prominent in the region underlying the hydathodes, so that a section cut near the margin and parallel to the midrib has a scalloped appearance (Pl. 27. fig. 13). The edges of the pinnules show minute teeth, one of which is illustrated in Pl. 27. fig. 14, whilst a section of the pinnule ending bluntly and presumably cut in a plane between two teeth is shown in Pl. 27. fig. 15. Like the midrib, the lateral veins of the pinnule are endarch for the greater part of their length and are surrounded by a sheath of thickened cells. As they approach the margin, however, they become mesarch (Pl. 27. figs. 9 & 10), and the individual tracheids become progressively shorter until they are shortly oval. This change in shape is accompanied by a change in the character of the thickening, this, in most instances, being closely reticulate. Where the pitted form persists, the elongated pits are replaced by short ones. The bundle meanwhile increases in diameter (Pl. 27. figs. 9–11), and finally expands to form a terminal hydathode composed of very large, irregularly oval, and relatively thin-walled tracheids in which either reticulate thickening or oval pitting occurs (Pl. 27. figs. 11 & 12). As the hydathode is approached, the sheath of thick-walled cells surrounding the bundle thins out and finally disappears, so that the hydathode itself is enclosed only by a layer of rather flat parenchymatous elements. We have been unable to detect a definite pore by which the hydathode communicates with the atmosphere, though it is possible that such a pore was present.

The lower epidermis consists, like that of the upper surface, of small cells with dark contents, but differs in being provided with abundant stomata which lie in the concavities between the veins (text-fig. 7 *a*) and in bearing both hairs and scales of an interesting type. The stomata are, in many instances, exquisitely preserved (Pl. 27. fig. 2) and it has consequently been possible to make a detailed study of them. The walls of the guard-cells, unlike those of the majority of the epidermal cells, are crisply defined, this being due presumably to the fact that they have undergone some degree of cutinisation. Each guard-cell has a thicker strip of cutinised wall in the pore area, and the cuticle itself is prolonged into a small but well-defined cuticular beak (text-fig. 7 *e*). The lumen of each guard-cell has roughly the shape of a bent dumb-bell, the two dilated ends being linked by a curved narrow canal which follows the contour of the pore (text-fig. 7 *d–g*). Stomata cut in various planes are shown in text-fig. 7 *b–g*, whilst a number seen in surface-view are

TEXT-FIG. 7.

d. [148·6]

b. [148·2]

c. [148·2 *]

g. [148·4]

e. [148·7]

f. [148·5]

a. [148· 83]
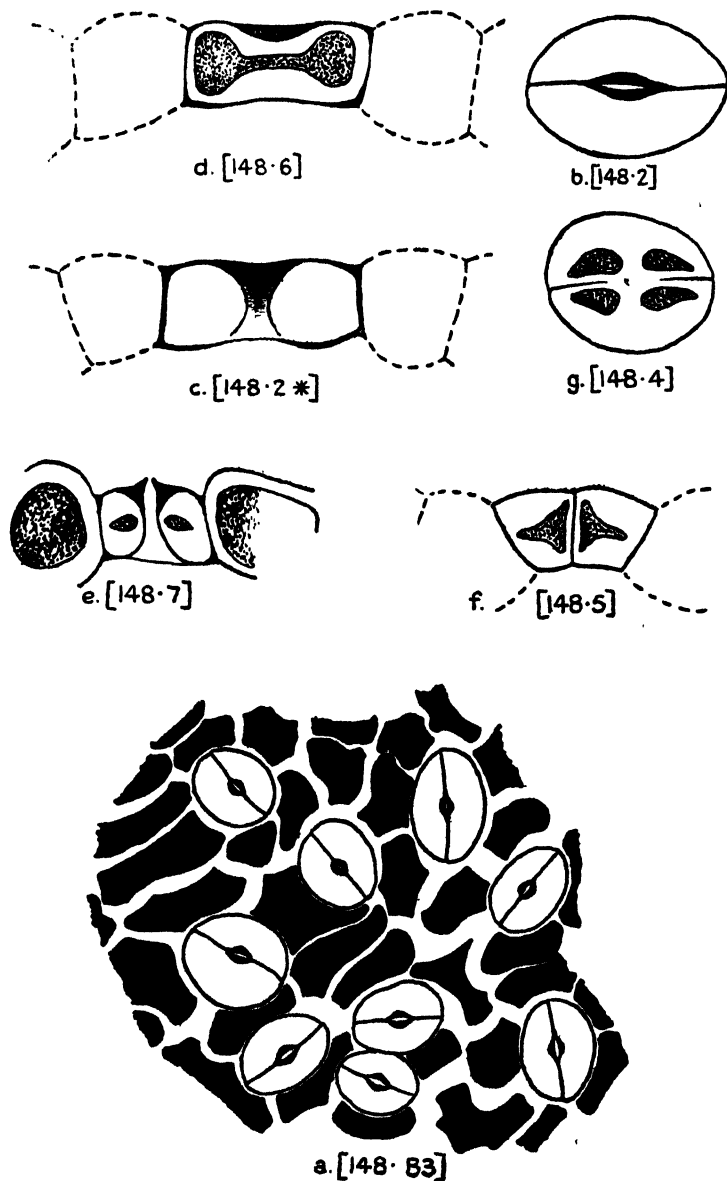
Surface and various sectional views of stomata.

a. Lower epidermis with stomata, × 400; *b.* A single stoma in surface-view at the same
magnification as *c–g*; *c.* A median section passing through the stomatal pore longi-
tudinally; *d.* A section cut through one guard-cell; *e.* Transverse section of a stoma
showing the guard-cells and cuticular beak; *f.* Transverse section of a stoma not
passing through the stomatal pore; *g.* Horizontal section of a stoma. *b–g*, × 700.

shown in text-fig. 7 a. This last also serves to illustrate the irregular shape of the epidermal cells which results from the presence of the stomata. Both hairs and scales are confined to the ridges of tissue lying below the midrib

TEXT-FIG. 8.
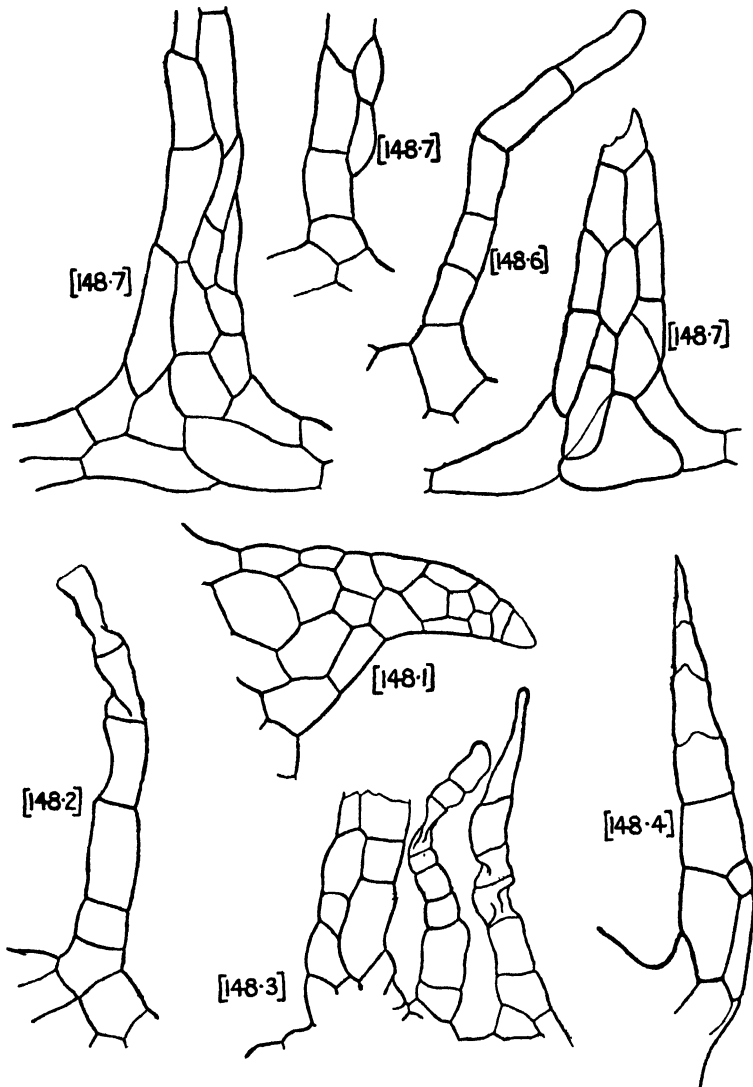
Hairs of various types from the lower epidermis of pinnules. All × 350.

and its branches. In the simplest cases they consist of a single, or in a few examples locally double, row of cylindrical cells, some of which have undergone

collapse. In other examples the base is multicellular, whilst the apical part consists, as in the previous type, of a single row of cells. In yet a third type the hair is a stout multicellular structure more or less circular in transverse section (text-fig. 8). The flattened scales or ramenta are less abundant than the hairs. They occur on both the fertile and sterile pinnules and are largely confined to the midribs. Each ramentum is about seven cells wide at its greatest width and narrows to a slender point. The cells constituting the margin are prolonged to form acutely pointed serrations (Pl. 27. figs. 18 & 19), whilst the basal region is several cells wide (Pl. 27. fig. 17). The actual apex consists of a single elongated pointed cell usually bearing a smaller cell of similar character projecting at an angle from near its base. In view of the opinions held by Bower (1923) and others as to the origin of ramenta it is a point of interest that hairs two cells wide throughout their length occasionally occur, which suggest an incipient attempt to form a flattened scale (Pl. 27. fig. 16).

(d) *The flattened axis.*—The best sections of the flattened axis occur in slides 148.5 and 148.6. Of these 148.6 is cut below the other, and the two together yield valuable information as to the departure of smaller lateral traces. The axis consists of a flattened mass of xylem partly surrounded by a sclerenchymatous cortex : no other tissues are preserved (text-fig. 9). The tracheids which constitute the xylem show scalariform pitting in the parts where its nature can be detected. It is reasonably clear that the axis was traversed by a continuous C-shaped strand with the xylem somewhat incurved at the free margins. It thus resembled the leaf-traces characteristic of *Psaronius* (Hirmer, 1927 ; Rudolph, 1905 ; Scott, 1920). Measurements of the xylem give a total length of approximately 1·0 cm., and its reconstruction as a C-shaped strand shows that this must have had a diameter of about 0·3 cm. A camera-lucida outline of the section in 148.6 is shown in text-fig. 9, and from this it will be seen that two daughter-traces, which are indicated in solid black, are being given off extra-marginally. These traces are of the same dimensions as those of the rachis bundles known to belong to *Scolecopteris Oliveri*. In 148.5 the one to the right is completely free and the gap caused by its departure has been bridged, whilst that on the left is still attached by one margin to the parent trace (text-figs. 10 & 11). This method of emission is in direct contrast to that of the pinnule trace of *S. Oliveri*, which, as has already been indicated, is marginal. Bower (1923), however, states that, whilst a constant type of pinna and pinnule trace departure is characteristic of the majority of ferns, sometimes both conditions are represented in the same species (e.g. *Trismeria trifoliata*). In this fern the extra-marginal mode of departure is represented in the vascular supply to the lower pinnae and the marginal in that of the pinnae situated nearer to the tip of the leaf. It is possible that *Scolecopteris Oliveri* may have shown the same peculiarity.

Whilst we consider that there is some likelihood of this axis belonging to *S. Oliveri*, it is realised that, in the absence of material showing actual con-
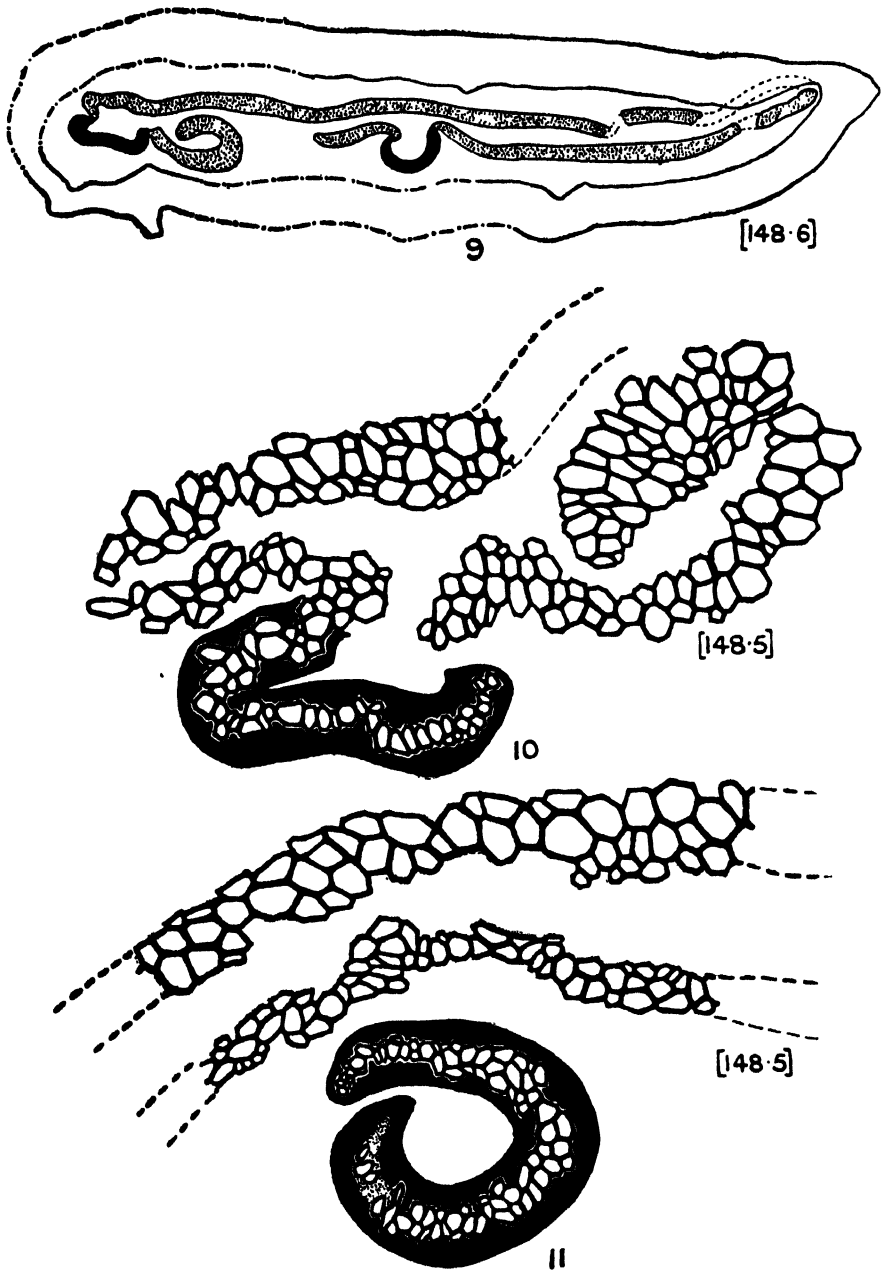
Fig. 9.—Camera-lucida outline of a transverse section of the crushed axis. The xylem, except for the extra-marginal traces which are in solid black, is stippled. × 10.

Fig. 10.—Later stage in the departure of the trace shown on the left of fig. 9. × 60.

Fig. 11.—Later stage in the departure of the trace shown on the right of fig. 9. × 60.

nection between axis and rachis, its assignation to that species rests upon a very slender basis. Association in the same matrix signifies very little, the character of the tracheidal pitting is not distinctive, and the method of departure of the lateral traces differs. The similarity in shape and dimensions of the lateral traces is probably the only evidence to which any weight could be attached.

DISCUSSION.

As has already been indicated in Part I. of this investigation (Scott, 1932), the reproductive organs of *Scolecopteris Oliveri* show well-marked differences of dimension and detail when compared with those of *S. minor* and *S. elegans*, the only other species of which petrified material has been studied. Whilst a detailed study of the vegetative parts of *S. elegans* has not been possible, sufficient detail has been made out from Strasburger's slide and from the polished block crowded with fertile pinnules (which has been courteously placed at our disposal) to show that the pinnules are smaller, relatively more elongated, and thinner in texture than in the Autun species, whilst the downward flexure of the margins is more pronounced. If Hirmer's assignation (Hirmer, 1927) of the structural material to *Asterotheca arborescens* is correct, then a further distinctive feature is available, since the venation in *A. arborescens* shows a strong median vein extending to the apex of the pinnule giving off opposite or sub-opposite unbranched lateral veins extending to the margin of the pinnule (Kidston, 1923-25, p. 485). No hydathodes appear to have been present. The anatomy of the rachis is not known.

With regard to *Scolecopteris minor*, more data are available (Hoskins, 1926). There is an obvious general similarity between the anatomy of the rachis in this species and that of *S. Oliveri*, both having an undivided U-shaped bundle from which marginal strands are detached to supply the pinnules. There are, however, definite differences in the cortical tissues, these, in the American species, consisting almost wholly of cells with relatively slightly thickened walls, some of which are large and of a secretory nature. A slender prolongation of this tissue passes into the concavity of the bundle. In *S. Oliveri* the cortex is differentiated into a sclerised bundle-sheath with a stout buttress projecting into the U-shaped trace and an outer zone of parenchyma. The pinnules of *S. minor* also differ from those of *S. Oliveri* both in their venation and in their general anatomy. The midrib ' consists of a small circular group of tracheids', and, though it is not evident from Hoskins's figure (pl. xxiv. fig. 10) whether this extends to the apex of the pinnule or not it gives off markedly alternate simple veins which pass to the pinnule margin without dilatation to form hydathodes. The epidermis bears multicellular hairs which are ' sparingly present on the lower side of the rachis and pinnules ' (Hoskins, 1926). Hoskins does not, however, describe these in detail. The mesophyll in *S. minor* consists of one or two rows of somewhat thick-walled hypodermal cells, below which is a row of thin-walled cells and in some sections ' a slight development of palisade tissue '. The characteristic

features of the three species, apart from the spore-containing structures, may be summarised as follows :—

S. Oliveri.	S. minor.	S. elegans.
Pinnule attached to rachis by whole width of base.	(?).	As in S. Oliveri.
Margin of pinnule flexed downwards.	As in S. Oliveri.	Flexure more pronounced than in S. Oliveri.
Midrib not extending to apex of pinnule, but branching dichotomously in distal part.	(?).	Midrib extending to apex of pinnule.
Lateral veins slightly alternate or sub-opposite, dichotomising near base with branches rarely forking again. Each branch ending in a hydathode.	Lateral veins markedly alternate, unbranched ; not ending in hydathodes.	Lateral veins opposite or sub-opposite, unbranched ; not ending in hydathodes.
Pinnules fleshy in texture.	Pinnules probably hard textured.	Pinnules thinner than those of S. Oliveri.
Hairs and flattened scales common.	Hairs sparingly present.	(?).
Rachis bundle U-shaped, giving off smaller C-shaped bundles marginally to the pinnules.	Rachis bundle U-shaped, giving off smaller rounded bundles marginally to the pinnules.	(?).
Cortex differentiated into sclerised inner and parenchymatous outer zones.	Cortex composed of practically uniformly thickened cells, some of which are secretory.	(?).

It will be observed that the venation in all three species is of the open type, that is, that there are no lateral anastomoses, this being a feature which is characteristic of the great majority of palaeozoic pinnules (Bower, 1923). It will be also evident that the system is readily derivable from a dichotomous condition. The variants illustrated by the species of *Scolecopteris* under consideration can all be matched by other forms included among the pecopterids and allied types. It is interesting to note that venation of a similar open character occurs in all existing marattiaceous genera, with the exception of *Christensenia* in which webbing is present. The occurrence of hydathodes is a feature which is not uncommon in the pinnae (or pinnules) of both recent and extinct species, and, so far as our observations go, there is a close similarity in all the examples studied. They were described for existing ferns as long ago as 1859 by Mettenius (1859), whilst Renault (1883) noted their occurrence in a number of fossil forms and described them accurately. Their occurrence in recent and fossil species was also recorded by Potonié (1892), who figures in surface-view a pinnule of *Pecopteris hemitelioides* from the Rothliegenden of Ilmenau, in which they are clearly shown. They are readily seen in many

species of *Blechnum* (e. g. *B. capense*, *B. punctulatum*, *B. Spicant*), in *Polypodium vulgare* and in *Coniogramme japonica*. Sections illustrating their structure are figured by Renault (1883) in *Pecopteris Nathorsti*, *P. subcrenulata*, *Scaphidopteris Gillioti*, and *Lageniopteris obtusiloba*. This last species, it is interesting to note, also resembles *Scolecopteris Oliveri* in the fleshy texture of its pinnules and in the presence of numerous stout multicellular hairs along the course of the veins on the under side of the pinnules. Curiously enough, the pollen grains which Renault figures as commonly present in association with *Lageniopteris* (1883, pl. xxiii.) are also present in considerable numbers in our slides.

The dermal appendages of *Scolecopteris Oliveri* are remarkable both for their variety and for the fact that included among them there are typical ramenta. Bower (1923, 1926, 1926 *a*) has produced evidence to show that among groups of ferns recognised on other grounds as primitive, hairs alone are present in many cases whilst ramenta tend to be restricted to the more advanced groups and to the more advanced genera of primitive groups. Thus hairs alone are present in *Marattia* and *Angiopteris*, whilst of the remaining Marattiaceae, *Christensenia* and *Danaea* have peltate scales in addition, and *Protomarattia* and *Archangiopteris* possess typical ramenta. *Scolecopteris Oliveri* thus shows, in this particular feature, a relatively advanced condition.

It will be realised that whilst there are grounds for regarding the flattened axis described in this paper as probably referable to *Psaronius* its identification as part of the vegetative system of *Scolecopteris* rests upon very slender evidence. If that evidence should be subsequently strengthened the vegetative characters may be considered to lend further support to the view that the affinities of *Scolecopteris* are with the Marattiaceae. Until, however, such evidence is available the inclusion of the genus within that family must rest largely on the nature of the reproductive organs.   '

ACKNOWLEDGMENTS.

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SCOLECOPTERIS OLIVERI.
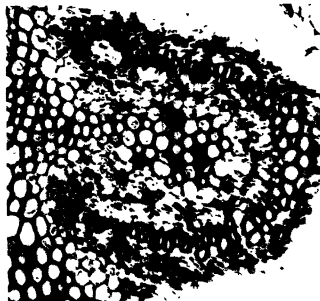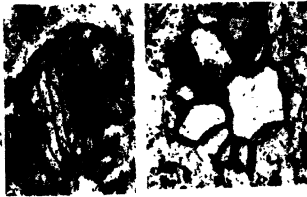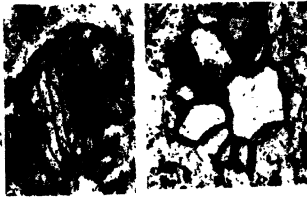
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EXPLANATION OF PLATE 27.

(All the figures are from untouched negatives. The matrix has been
blacked out from the prints used for figs. 3 & 5.)

Fig. 1. Superficial section of the distal portion of a pinnule showing the venation. The stomata are shown as dark spots between the veins. ×15. (Slide no. 148.2.)

Fig. 2. A small part of the same pinnule showing the stomata more highly magnified. ×200. (Slide no. 148.2.)

Fig. 3. Transverse section of the rachis showing the U-shaped bundle and the general distribution of the tissues. ×20. (Slide no. 148.B7.)

Fig. 4. The bundle of the rachis more highly magnified. Note the marginal pinnule traces. ×75. (Slide no. 148.B7.)

Fig. 5. Transverse section of a pinnule showing an unequal development of aqueous tissue. ×40. (Slide no. 148.6.)

Fig. 6. Transverse section through the reflexed margin of a pinnule showing a hydathode and a hair arising from the lower epidermis. ×40. (Slide no. 148.6.)

Fig. 7. Transverse section through a pinnule in a plane parallel to the midrib showing a dichotomising lateral vein. ×40. (Slide no. 148.4.)

Fig. 8. Transverse section through the midrib of a pinnule showing the C-shaped character and the sheath of thick-walled cells. Note the collapsed protoxylem lining the concavity of the trace. ×100. (Slide no. 148.B5.)

Fig. 9. Transverse section through a lateral vein approaching a hydathode. Note that it is mesarch. ×150. (Slide no. 148.6.)

Fig. 10. Transverse section through a lateral vein at the proximal end of a hydathode ×150. (Slide no. 148.6.)

Fig. 11. Transverse section through a hydathode. Note the shape of the tracheids and their pitted walls. ×150. (Slide no. 148.6.)

Fig. 12. Longitudinal section through a hydathode. ×150. (Slide no. 148.B2.)

Fig. 13. Marginal section through a pinnule showing four hydathodes. ×50. (Slide no. 148.5.)

Fig. 14. Transverse section of a pinnule showing a minute tooth. ×40. (Slide no. 148.B1.)

Fig. 15. Transverse section of the edge of a pinnule ending bluntly. ×50. (Slide no. 148.B6.)

Fig. 16. A hair composed of two rows of cells from the midrib of a fertile pinnule. ×150. (Slide no. 148.B5.)

Fig. 17. Basal part of a detached ramentum in surface-view. ×120. (Slide no. 148.B1.)

Fig. 18. Ramentum attached to the midrib of a fertile pinnule. ×120. (Slide no. 148.B3.)

Fig. 19. Portions of ramenta. Note the marginal teeth. ×120. (Slide no. 148.B3.)

Fig. 20. Transverse section of a ramentum. ×150. (Slide no. 148.B5.)

Contributions to our Knowledge of the Colonial Volvocales of South India. By M. O. P. IYENGAR, M.A., Professor of Botany, Presidency College, Madras. (From the Department of Botany, East London College, University of London.)

(PLATE 28, and 10 Text-figures.)

[Read 19 January 1933]

THERE appears to be a general impression among algologists that the colonial members of the Volvocales are pre-eminently cold-water types (West, 1916, p. 429). This impression arises from the fact that so far only very few members of this group have been recorded from the warmer parts of the globe, and it has naturally been assumed that these records represent sporadic occurrences. The object of this paper is to record and describe the colonial Volvocales collected within a small area of Southern India *, and to draw attention to the common occurrence of these forms in a typically tropical area. I have no personal familiarity with the occurrence of the colonial Volvocales in Northern European countries, and am therefore not in a position to compare their numbers there and in the Tropics, but when viewing the abundance of these forms in India have often wondered whether they could ever attain to such profusion in the colder waters of the temperate zones.

Remarks on the Occurrence of the Colonial Volvocales.†

Colonial Volvocales have been met with in many different kinds of waters in Southern India, such as large reservoirs and tanks, ponds and permanent pools, paddy-fields, water-tubs, and brackish water-canals. Though occurring commonly in these habitats, it is in the innumerable temporary rain-water pools found during the wet seasons, both by the roadside and in the open country, that they attain to maximum abundance. There are two wet seasons in India, the summer or South-West monsoon from June to the middle of September, and the winter or North-East monsoon from the middle of October to December. The weather during these rainy months is comparatively mild, and the sky cloudy for long periods during the day.

Numerous Volvocales are found in these small pools, often occurring in such large numbers as to give the water a green colour. The depth of the green colour usually depends upon the density of the algal population, and

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* An account of a species of *Volvox* from Lucknow in North India is included in this account.

† I have already mentioned some of the following points in a previous paper (Iyengar, 1920).

is often found to change in the same spot at different times of the day, especially if the day is bright. This is due to the upward and downward movement of the forms involved, in response to the decreasing or increasing intensity of the light. They aggregate near the surface in the morning and evening, and retreat below the surface in the middle of the day when the light becomes too strong. They also appear to move downwards at night, as they are not to be found at the surface during the early morning hours. Smith (1917, p. 178) observed similar upward and downward movements on the part of *Volvox mononae* at different times of the day in Lake Monona, in response to the varying intensity of the light.

These organisms exhibit a somewhat similar behaviour, even in the diffuse light of the laboratory. Kept in a green vessel in the middle of a room lighted from a window on one side, they collect on the side directed towards the light during the morning and evening hours, but, during the middle of the day when the light is strongest, they recede to the side of the vessel farthest from the window. This movement was observed even in material placed in a watch-glass. Many observers have referred to similar phenomena (Oltmanns, 1922–23, pp. 371–372), both in nature and in the laboratory, but it may not be without interest to record these observations made in a tropical environment.

Another set of observations appear to be explicable as being determined by the need for an adequate air-supply. In certain pools in the sandy beach at Madras, numerous Volvocales (*Chlamydomonas* spp., *Gonium pectorale*, *Pandorina morum*) and Diatoms were to be found in the water. But, in addition, the sand was green to a distance of one or two feet from the edge of the pools, forming as it were a green border around them. The first impression obtained was that the algae had been left behind by the drying up of the pool. When some of the green sand was shaken up with water, however, the latter became green, and when a drop of it was examined under the microscope, countless forms identical with those occurring in the pools were observed actively swimming in the water. When a few particles of the wet green sand were mounted under the microscope, large numbers of the algae could be seen swimming in the thin film of water surrounding each particle. It was found that the algae in the pool were not so active as those in the films around the sand-particles, and it seemed that the latter were definitely in a healthier condition. The thin films of water around the sand-particles were, of course, in direct contact with the air in the interspaces of the sandy soil, and it is to be presumed that they were richer in dissolved air than the water of the pool itself. Evidently the algae favoured this situation with its presumably better aeration. Such sand-algae (*Chlamydomonas* and Diatoms) have been observed by Warming (1909, p. 175) on the coasts of Denmark and by Cowles (1899, p. 114) on the coasts of Lake Michigan.

Among the unicellular genera that were collected in South India with more or less frequency are *Chlamydomonas*, *Carteria*, *Chlorogonium*, *Lobomonas*, *Phacotus*, *Pteromonas*, and *Pyramidomonas*, while the colonial members are

represented by *Chlamydobotrys*, *Gonium*, *Pandorina*, *Eudorina*, *Pleodorina*, and *Volvox*. These algae are very usually associated with species of *Euglena*, *Trachelomonas*, and other Flagellata. The present account deals with the colonial forms. It is hoped to publish an account of the unicellular Volvocales at a later date.

Apart from their occurrence in the rain-water pools, the Volvocales are also found in bigger pieces of water, but here they occur sparsely among other algae. *Volvox*, which is of rare and sporadic occurrence in India, has, however, never been collected in the temporary rainwater pools. It seems to prefer deeper and more permanent waters. As regards the other forms, they evidently find, as in other parts of the world, optimum conditions for growth in the fresh rain-water (with its high percentage of dissolved oxygen) and under the diminished light-intensity of the monsoon periods. They occur in greater profusion during the summer monsoon than during the winter monsoon months, which suggests that it is the higher temperature of the former that favours the growth of these algae. During the summer monsoon the highest shade temperatures for Madras in 1919 were 105°·0, 102°·2, 101°·1, and 99°·0 F. for June, July, August, and September respectively, while during the winter monsoon they were 96°·2, 90°·6, 86°·3 F. for October, November, and December respectively. This effect of temperature indicates that the Volvocales are more likely to attain to maximum abundance in the Tropics than in the colder regions of the globe.

The rain-water pools are often very muddy, since buffaloes and other animals tend to wallow in the water during the warmer parts of the day. The muddiness does not seem to affect the algal population, since as the water clears the algae again become visible, and once more impart to it a greenish colour. The churning up of the water by the wallowing animals may help in the solution of the mineral salts, and the muddiness may also afford the algae a certain amount of protection against strong insolation in the middle of the day.

SYSTEMATIC ENUMERATION OF THE COLONIAL VOLVOCALES OF SOUTHERN INDIA

The following account deals with the colonial Volvocales, both from the taxonomic and morphological points of view. No complete description of the previously known forms is given, but under each species a number of independent observations are described, which either confirm earlier work or appear to extend our knowledge of the form in question. The preliminary observations were usually made on the living algae, although the investigations were subsequently completed on preserved material.

SPONDYLOMORACEAE.

CHLAMYDOBOTRYS STELLATA Korschikoff. (Text-fig. 1, A, B, D–F.)

This alga, which has not been before recorded from India, is very rare. It was collected near Bangalore by Dr. Sampathkumaran, who kindly handed

me the material. I subsequently found the same species on two occasions in rain-water pools in Madras.

Colonies with eight and with sixteen cells were usual (text-fig. 1, B, A), the former possessing two tiers and the latter having four tiers of four cells each. The cells of successive tiers alternate with one another. In each tier, however, the four cells are not at the same level, one diagonally opposite pair of cells being placed at a slightly higher level than the other diagonal pair. Very occasionally four-celled colonies are found (text-fig. 1, F). Each cell has two cilia and two contractile vacuoles. In one preserved specimen in which a good view of the anterior end was obtained, the protoplast appeared to be slightly beaked, the two cilia arising from this point (text-fig. 1, E). No pyrenoids were evident. The cells are pear-shaped, with the broader end anterior, the narrow, backwardly directed posterior end being very sharply conical. This conical posterior end was clearly seen on staining with dilute aqueous methylene-blue. The first impression obtained is that the contents of the cells have contracted away from the posterior extremity, but careful examination shows that the apparently empty area is solid, the thickening here showing some lamellation (text-fig. 1, A, B, D–F). Previous authors who have dealt with this form have assumed that the hyaline area at the posterior end was due to contraction of the protoplast.

The colonies during their forward movement rotate on their axes, the rotation being clockwise from right to left. No reproductive stages were observed.

A sixteen-celled colony measured 30·5 μ broad and 39 μ long, the cells being 9 μ broad and 12·5 μ long.

VOLVOCACEAE.

GONIUM PECTORALE Müller.

This alga is fairly common, especially in fresh rain-pools in the sandy beach at Madras. The colonies are composed of four, eight, or sixteen cells.

PANDORINA MORUM Bory.   (Text-fig. 1, C, G–M, Q–T.)

This occurs very commonly in rain-water pools, often intermingled with other motile algae, but is also found in larger pieces of water.   The forward movement of the colonies, accompanied by the usual rotation, takes place with a series of very slight jerks, the posterior portion of the colony oscillating slightly from side to side, while the anterior portion remains steady.

The colonies, though usually sixteen-celled, quite frequently consisted of only eight cells.   They were very slightly broader at the anterior than at the posterior pole.   The cells were arranged in alternating zones of four cells each, there being four in sixteen-celled and two in eight-celled colonies. The somewhat pear-shaped cells were arranged very compactly in the living specimens, so that they were slightly angular through mutual pressure.   In living material the enveloping mucus-sheath is well seen in young coenobia, but in the older ones it appears to fit closely over the cells, so that it is some-times difficult to see it clearly.   In preserved formalin material, on the other hand, when the cells through contraction appear more rounded, the mucilage is equally evident in both young and old specimens.

There was usually a single pyrenoid in each cell, but in some *very old* colonies the cells contained from one to four pyrenoids.   The eye-spots were very large in the front zone cells and gradually diminished in size in the others (text-fig. 1, C, G).   In one coenobium the eye-spots in the front zone were 3μ in diameter, in the second zone 2μ, in the third zone about 1μ, and in the fourth zone a hardly visible speck.   The eye-spots are round in surface-view, but when seen in profile are concavo-convex with the concavity directed outwards.   In the individual cell the eye-spot is situated close to the hyaline anterior region where the cilia arise, but on the side remote from the anterior end of the colony.   The eye-spots of the four anterior cells, as seen from the end, are placed more or less equidistantly with reference to the circular contour of the colony (text-fig. 1, I).   This position enables them to have good exposure, not only to the light from the front, but also to that coming from the side. The eye-spots of the four posterior cells occupy a similar position as seen from the posterior end (text-fig. 1, J).

Conjugation was observed once (text-fig. 1, H, L, M, Q–T).   The naked gametes were of different sizes, the smaller measuring on the average 12μ and the larger 16μ in diameter.   Conjugation took place in one of three ways, viz. (1) between a large and a small gamete (text-fig. 1, Q), (2) between two large gametes (text-fig. 1, R), or (3) between two small ones (text-fig. 1, H, M). These observations agree with those of previous workers.   The zygotes with four cilia, two eye-spots and two pyrenoids, remained motile for some time, and, finally, came to rest (text-fig. 1, R. S) ; their further development was not observed.

The full-grown sixteen-celled colonies measured $61 \times 48 \mu$, $52 \times 44 \mu$; dimen-sions of the cells, $16 \times 24 \mu$, $11 \times 16 \mu$, $18 \times 22 \mu$.

One can distinguish two forms in the previous records of *Pandorina morum* ;

the one with globular coenobia and somewhat rounded cells and a broad gelatinous margin to the envelope ; the other with oblong-ellipsoidal coenobia, the cells very compactly aggregated and angular, and with a narrow, but firm margin to the envelope (cf. the figures of Smith and Conrad reproduced in Pascher, 1927, figs. 387 and 388 respectively). The Indian alga belongs to the latter type, which may be named f. *oblonga* (cf. Stein, 1859–83, whose Tab. 16, figs. 14 & 15, may be regarded as f. *oblonga*), the former being described as f. *typica*.

PANDORINA MORUM, forma MAJOR, n. f. (Text-fig. 1, N, O, P, U, V ; Pl. 28. fig. 7.)

This alga was found on one occasion in enormous numbers, giving the water of a rain-water pool a green colour. The colonies were fairly big for *Pandorina*, and normally contained thirty-two cells, though a few with sixteen cells were also found. The chief characteristic lay in the invariable presence of three or four pyrenoids in each cell, no matter whether the colony contained thirty-two or sixteen cells (text-fig. 1, N, P, U). The pyrenoids are formed *de novo* (cf. p. 330). The colonies were ellipsoidal with rounded ends, the anterior pole being broadly rounded, while the posterior one was slightly truncate. The cells were arranged in five zones comprising 4, 8, 8, 8, and 4 cells respectively, the cells of the successive zones alternating with one another. This is the arrangement found in *Eudorina elegans*, but here the cells were pear-shaped (text-fig. 1, P) with the pointed end directed inwards, and were placed very compactly, so that in a surface-view, in a living specimen, they had an angular appearance. In the preserved material from which the drawings were made, the cells were somewhat contracted, and were more rounded at the corners (text-fig. 1, U, V).

Playfair (1915, pp. 336–7 and pl. 44. fig. 18) has described a similar form under the name of var. *tropica*. He did not recognize the *Eudorina*-like arrangement of the cells. He describes them as being arranged in a ' central ring of 10, above and below which is a rosette of 6 plus 1 ' (in planes parallel to the longitudinal axis of the colony). His figure, when examined carefully, however, shows the arrangement found in *Eudorina elegans* and in the alga here described. There are, in his figure, two cells at either end which represent the two upper cells of the anterior and the posterior tiers of four cells. The second, third, and fourth rows (lying at right angles to the longitudinal axis) consist of four or five cells each, being the cells visible from above of the second, third, and fourth tiers, each of which consists of eight cells.

Pandorina morum has been described (Stein, 1859–83, Abth. iii. 1, tab. 18, fig. 1 ; Pascher, 1927, p. 423, footnote) * as sometimes consisting of thirty-two cells, and the occurrence of more than one pyrenoid in each cell has also been

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* Stein figures a thirty-two-celled colony with one pyrenoid in each cell. Pascher states that occasionally the number of cells in the colony is eight or thirty-two, or very rarely even four or two.

reported. But in the alga just described the normal number of cells is thirty-two, and more than one pyrenoid is always to be found in the cells of the full-grown colony. Playfair (1915) does not give any details of the cell-structure of var. *tropica*, and it is not clear from his figures how many pyrenoids there were in each cell. The constancy of these features in my material inclines me to consider it as a distinct form of *Pandorina morum*. Specimens of the type-species (with a single pyrenoid in the cell) did not occur in the collection. Similarly, in the gatherings of the type-species, not a single individual of this form was encountered. In such collections, however, certain very old specimens had two to four pyrenoids in the cells. In the same way, in very old specimens of the form under consideration, I found cells with as many as six to eight, and in one case even twelve to thirteen pyrenoids (text-fig. 1, O). In such specimens the cells were very nearly rounded, and these colonies possessed a definite *Eudorina*-like appearance.

Perfectly young colonies of the form under discussion always had a single pyrenoid in the cells (text-fig. 3, B). As the colonies grew older, more pyrenoids were formed, and they were formed *de novo*. In no case was the original pyrenoid observed to divide. The new pyrenoids make their appearance as hazy round bodies, which gradually increase in size and finally take a definite form. The newly formed pyrenoid is much smaller than the original single one. The pyrenoids arise successively, and when three or four pyrenoids are present they are generally of slightly different sizes and the original pyrenoid can be distinguished for a long time by its larger size. The type with a single pyrenoid may be considered as more primitive, and the form which *normally* has a larger number of pyrenoids as the more advanced.

The dimensions of the full-grown thirty-two-celled colonies were 55–64 μ broad and 63–74 μ long (55×64 μ, 57×63 μ, 57×68 μ, 61×68 μ, 64×74 μ). The cells measured 11–15 μ in breadth and were 12–14·8 μ long.

EUDORINA ELEGANS Ehrenberg. (Text-fig. 2 ; Pl. 28. fig. 17.)

This occurs in smaller and larger pieces of water among bigger algae and as stray individuals in the plankton, but it is found in the greatest profusion in the rain-water pools, to the water of which it very often imparts a green colour. Most of my observations confirm what has already been recorded, but a certain number of supplementary data are given in the following. The coenobia are generally elliptic-oblong to broadly elliptic. Very often the anterior pole is broadly rounded, while the posterior one is somewhat truncate (text-fig. 2, A, L). The rotation of the colonies during forward progression is generally in a clockwise direction as seen from the anterior end, but the same colony may quite often rotate in the opposite direction. Grove (1915) found the individuals of *Eudorina illinoisensis* (*Pleodorina illinoisensis* Kofoid) collected in Great Britain showing clockwise rotation, unless their movement was in some way obstructed, when as they receded they rotated in the opposite direction, Carter (1858, p. 238) observed rotation in both directions in *Eudorina*

colonies from Bombay, and Kofoid (1898, pp. 282–3) made the same observation on his material of *Eudorina illinoisensis*.

In my material I very often found a few stray colonies *moving without any rotation whatever*, their movement being so striking that it always arrested my attention. The movement was usually very rapid, compared with the normal rotating colonies. The cause of this peculiar movement has not been elucidated.

The eye-spots were concavo-convex with the concavity directed outwards, and, as has often been described, were largest in the four cells of the front tier and became smaller and smaller towards the posterior end, sometimes being so small as hardly to be seen.

The cells of thirty-two-celled colonies were arranged in the familiar five tiers of 4, 8, 8, 8, and 4 cells from front to back, the cells of the three middle rows alternating with one another. In the sixteen-celled colonies there are four tiers of four cells each and the cells of the four tiers alternate with one another.

Each cell has a very thick wall which consists of a broad gelatinous portion on the outside (text-fig. 2, B, *o*) and a thin, comparatively firm innermost layer (text-fig. 2, B, *i*) immediately next to the protoplast (cf. p. 336). The cell-walls are seen clearly on staining with dilute methylene-blue or toluidine-blue.

The colonies vary very much in their general appearance. In some the cells are placed close together, as in text-fig. 4, A. In others the cells are more widely separated and a considerable area of clear gelatinous matrix is seen between them. Further, the cells may be placed either at a certain distance from the periphery of the colony or very close to the surface. In the latter case the bounding mucilage is often very compact and somewhat refractive, and the gelatinous matrix (of the formalin material) is readily stained by an aqueous solution of erythrosine, which does not colour the mucilage in the other types of colonies.

Mammillary processes were seen in living material on most of the colonies in a few collections, but in others none of the individuals showed this feature. This suggests that the presence of processes is characteristic of distinct races. The colonies possessing these processes were generally ellipsoidal and not subglobose.

In most specimens the boundary of the mucilage, when examined under high power, was seen to be slightly though definitely depressed just in front of each cell, about on a level with the point of exit of the cilia (text-fig. 2, D) ; a very similar condition is seen in Hartmann's figures of *Eudorina elegans* (Hartmann, 1921, tab. 1, figs. 3 & 4). This appearance is visible in living, as well as in preserved, material. In other living colonies the boundary of the mucilage appears to be slightly wavy following the contour of the cells (text-fig. 2, F), so that it is slightly bulged out opposite each cell ; this undulation was more pronounced towards the posterior end. It is possible that the posterior mamillose processes are simply an exaggeration of this feature.

TEXT-FIG. 2.
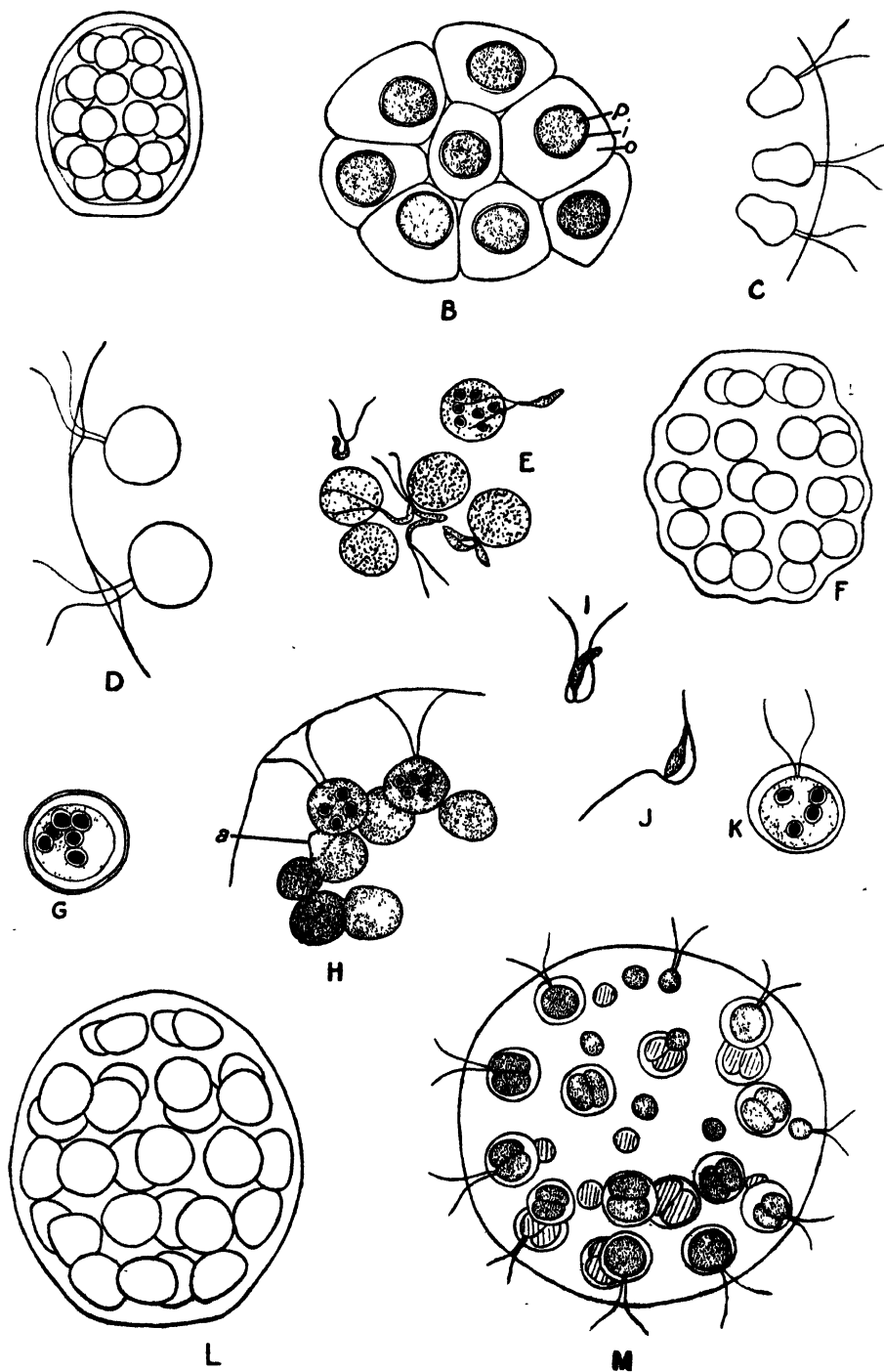
EXPLANATION OF TEXT-FIG. 2.

Eudorina elegans Ehrenberg.

A, F, L, different types of colonies. B, groups of cells showing the gelatinous walls : p, protoplast ; i, innermost layer of wall ; o, outer gelatinous layer of wall. C, portion of a colony with pyriform cells. D, small part of a colony showing a depression in the gelatinous envelope opposite each cell. E, spermatozoids swarming round ova. G, oospore. H, loosened ova in the diffluent mucilage of the colony ; cilia still present on two ova. I and J, spermatozoids showing motaboly. K, ovum before gelatinisation of the inner layer of the wall. M, colony with gonidia and somatic cells irregularly scattered.

(A & M, × 280 ; B, × 440 ; C, × 540 ; D, × 800 ; E & L, × 435 ; F, × 325 ; G–K, × 870.)

The shape of the protoplasts as observed in living material also varies somewhat. Usually they are spherical, but sometimes they are slightly broadened in a plane parallel to the outer surface of the colony. In some colonies the cells have the outer surface somewhat flattened, while the inner one is rounded, the cell in side view appearing somewhat hemispherical (text-fig. 2, L). In one colony, found during the examination of formalin material, the cells were elongated at right angles to the surface and somewhat narrowed towards the inside, with the inner and outer surfaces broadly rounded, so that the whole cell had a pear-shaped appearance (text-fig. 2, C). The cells distantly resembled old ones of *Pandorina morum* f. *major*, but they were arranged as in a typical *Eudorina*, being disposed separately in the periphery of the mucilage.

In the absence of pure cultures it is impossible to say whether certain of these forms could be regarded as distinct races. But it may be mentioned that most of the individuals of any single collection tended to conform to one particular type in respect of the crowded or scattered disposition of the cells, the general shape of the colonies (whether broadly or narrowly ellipsoidal or subglobose), the presence or absence of mammillary processes, the shape of the cells, etc. In every collection, however, there were usually a few colonies belonging to one or more of the other forms.

Whatever value these may have, they are of interest in suggesting possible steps in the evolution of *Eudorina*. Those forms in which the cells are crowded in the centre may be regarded as less advanced than those in which they are placed further apart and nearer the periphery. All my specimens of *Eudorina illinoisensis*—a decidedly more advanced form than *E. elegans*—conform to the second of these types.

Although all the cells of a colony of *E. elegans* may appear to be equal in size, a careful examination shows that, in most full-grown colonies, the four front cells are *very slightly* smaller than the rear ones. This fact has been recorded by Hartmann (1921, p. 227) and by Pascher (1927, p. 49) in European material. During asexual reproduction all the thirty-two cells sometimes form thirty-two-celled daughter-colonies, though sixteen-celled colonies are frequently formed, especially by the four front cells.

A single thirty-two-celled colony of *Eudorina elegans* was found, in which seventeen of the cells (i.e. about half) had enlarged and were undergoing their first divisions, while the remainder were quite small and evidently somatic (text-fig. 2, M). The gonidial and somatic cells were distributed without order throughout the colony, except in the foremost tier where three small cells could be recognised. This specimen resembles the two isolated colonies found by W. & G. S. West (1906, pp. 104–5, pl. 10. figs. 7 & 8) in the plankton of Lough Mawmeen in Ireland, although in these specimens the gonidia had not yet divided.

Sexual reproduction was observed in three different years. The colonies were always dioecious. In the male and female colonies all the cells usually became antheridia or oogonia, though a few cells occasionally formed daughter-colonies, especially one or more of the front four cells (Pascher, 1927, pp. 62, 436–7).

The first indication of commencing sexual reproduction is an increasing softening of the gelatinous matrix accompanied by a swelling of the colonies. The cells lie loosely in the soft mucilage and numerous foreign particles are seen adhering to its surface. In this condition the colonies float up to the surface in large numbers and form a green scum.

The antheridial clusters, after struggling for a while inside the loose gelatinous matrix of the parent colony, finally escape. Many of them were seen swarming round the female colonies and even round the individual oogonia, the soft condition of the gelatinous matrix of the female colony rendering the entry of the spermatozoid clusters easy. The individual spermatozoids of the clusters soon separate. They appear to undergo change of shape during movement, as the greatest width is found sometimes at one and sometimes at the other end of the body (text-fig. 2, I, J).

In female colonies approaching maturity the oogonia lie loosely in the softened matrix. In this condition they still retain the cilia and the firmer inner layer of the wall, although the gelatinous outer portion has by this time lost its individuality and become merged in the general matrix (text-fig. 2, K). Soon after, the remaining portion of the wall evidently gelatinises leaving the naked protoplasts of the ova, still bearing the cilia, embedded in the soft mucilage (text-fig. 2, H). At this stage they perform very slow oscillatory movements from side to side, or occasionally a short forward movement inside the mucilage. Finally, the cilia are lost and the ova become quiescent. Most of the ova are spherical, but in the preserved material some appeared to be slightly beaked, with an individual hyaline area near the beak suggesting a receptive spot (text-fig. 2, H, a).

During these changes numerous spermatozoids were swarming around the egg-cells and some were seen actively attacking the ova, although many were lying motionless next to them (text-fig. 2, E ; Pl. 28. fig. 17). Nevertheless, though they were kept under observation from 10 a.m., when the spermatozoid clusters generally escaped, until late in the afternoon when the sperms became

quiescent, no instance of actual fertilisation or any stage in fusion was seen. Since the spermatozoids became quiescent in the evening, they were not further observed during the night. But, on the next day, numerous egg-cells surrounded by definite and fairly thick walls were found in the material (text-fig. 2, G). Evidently fertilisation, if it took place at all, must have ensued during the night. Carter (1858, p. 240) likewise did not see the actual process of fertilisation in his Bombay material of *Eudorina*, though he found the spermatozoids swarming round the egg-cells. Merton (1908, p. 445) and Chatton (1911, p. 309) observed the same stages, but failed to see actual fertilisation, nor did Grove (1915, p. 177) observe it in *Eudorina illinoisensis*. Thus five observers have seen the stages leading to fertilisation, but none have observed the actual process. If Schreiber (1925, pp. 362–3) had not described the formation of four protoplasts in the germination of the zygote of *Eudorina*, which renders a reduction division and a previous fusion probable, one would be tempted to suspect parthenogenesis in *Eudorina*.

Dimensions.—Colonies 72–118 μ long and 60–102 μ broad (60 × 72 μ, 60 × 77 μ, 63 × 72 μ, 72 × 91 μ, 74 × 99 μ, 83 × 94 μ, 91 × 106 μ, 85 × 101 μ, 102 × 118 μ). Cells 11–19 μ in diameter. Oospores 19–23 μ in diameter.

EUDORINA ILLINOISENSIS (Kofoid) Pascher (*Pleodorina illinoisensis* Kofoid).* (Pl. 28. fig. 1.)

This alga is often found in large numbers in the rain-pools at Madras, generally associated with other Volvocales like *Eudorina elegans*, *Pandorina morum*, *Chlamydomonas* spp., etc. The colonies are ellipsoidal or somewhat subglobose, usually without mammillary processes. The movements are like those of *E. elegans*, described on p. 330.

The colonies usually contain thirty-two cells, but sixteen-celled colonies are frequently met with. In the young condition all the cells of a colony are very nearly equal, but in the older colonies the four anterior cells are always smaller than the others. In the colonies of a single collection, however, all gradations can be found between those in which the difference is slight and those in which it is well marked ; these differences are no doubt due to differences of age. As in *E. elegans*, the anterior cells possess the biggest eye-spots.

The cells of the young colonies contain only a single pyrenoid. As the cells enlarge more pyrenoids are formed, and, up to a certain stage, the number of pyrenoids increases uniformly in all the cells, generally until two to four are present. After that, pyrenoid-formation ceases in the four anterior cells, but continues for some time in the others, so that ultimately the remaining cells contain as many as nine or ten pyrenoids. The accessory pyrenoids are formed *de novo*, as in *Pandorina* and *E. elegans*. Grove (1915, p. 173) found the same features in his English material of *E. illinoisensis*, but states that the cells of the youngest colonies have no pyrenoids. The youngest

* Pascher, 1927, p. 443. With respect to the reference of *Pleodorina illinoisensis* to *Eudorina*, cf. p. 339.

colonies in my material, however, always showed a small pyrenoid in each cell.

Apart from the markedly smaller dimensions of the front cells, the remainder also usually show a gradual, though very slight, increase in size from the anterior to the posterior end. Thus, the cells of the third tier are slightly larger than those of the second, and those of the fourth are larger than those of the third. The cells of the fifth (the posterior) tier, however, are generally slightly smaller than those of the fourth and sometimes also exhibit a smaller number of pyrenoids. Grove mentions the gradual increase in size of the cells from the anterior to the posterior end, but states that often, though not always, the cells of the posterior tier are the largest in the colony. In all the colonies examined by me, however, the cells of the fourth tier were the largest in the colony.

Measurements of the cells of four colonies (in μ).

	Colony I.	Colony II.	Colony III.	Colony IV.
Cells of 1st tier	13·5–14	10·5–11·3	11–11·7	9·75–15·25
2nd ,, ...	17	11–16·5	14·5–18	17·25
3rd ,, ...	17·7	16·5	19·25	17·25
4th ,, ...	18·5	16·5	19·25	17·35
5th ,, ...	16·5	15·75	17·25–19	16·5

Kofoid (1898, p. 276) observed hexagonal reticulations round the cells of the colonies after treatment with aqueous methylene-blue. Grove (1915, pp. 171–2) makes the following remarks with reference to this feature :—
' I could not succeed in demonstrating any hexagonal reticulations round the cells with the methylene-blue which Kofoid recommends for the purpose, until I adopted the expedient of pressing upon the cover-glass so as to expel the cells ; then five rows of faintly outlined irregular hexagons could sometimes be detected. But this was an artefact, produced by the mutual pressure of the gelatinous capsules surrounding each cell at a certain stage.'

I was able to see such reticulations around the cells very distinctly, both in *E. elegans* and in *E. illinoisensis*, after treatment with either aqueous methylene-blue or aqueous toluidine-blue (text-fig. 2, B). The reticulation around each protoplast really represents the outer edge of the gelatinous layer of the cell-wall, which is bounded, immediately adjacent to the protoplast, by a fairly firm inner layer (cf. p. 331). When a colony is stained with aqueous methylene or toluidine blue, the outermost edge of the gelatinous layer takes up the stain quicker than the rest of the wall, and hence the more or less polygonal contour stands out rather prominently for some little time. Later, when the stain becomes more uniformly distributed, the reticulation is not so distinct. The reticulation is thus really due to the mutual pressure of the gelatinous walls of the cells upon one another, as Grove suggests, but it is not clear why he regards it as an artefact.

Sexual reproduction.—The distribution of antheridia and oogonia was not uniform. Some colonies were definitely male, others were monoecious. None were purely female. In the male colonies the four anterior cells either failed

to divide or underwent very slow division into a few cells, while the remaining cells formed antheridia. Sometimes a few of these latter divided to form sixteen-celled daughter-colonies. In the monoecious colonies, twenty-eight posterior cells became oogonia, while the four anterior cells usually developed into antheridia, but sometimes one (Pl. 28. fig. 1) or more, or even all, of them divided to form sixteen-celled daughter-colonies. Some of the twenty-eight posterior cells may develop full-sized (i.e., thirty-two-celled) daughter-colonies, but in none of the monoecious specimens examined did they give rise to antheridia or to sixteen-celled coenobia. Similarly, the four anterior cells never formed full-sized thirty-two-celled coenobia, not did they ever become oogonia. Grove's experience with his English material was similar.

Carter (1858, pl. 8, fig. 4) in the Bombay material of *E. elegans* observed the four front cells forming antheridia, while the remainder became oogonia, but this has not been recorded by any subsequent worker. His specimens were probably monoecious forms of *E. illinoisensis*.

The following are examples of a few of the colonies observed by me :—

(*a*) Monoecious colonies (28 oogonia in all cases).

Specimen 1. Front tier 4 antheridia.

,, 2. ,, 2 undivided cells, 2 antheridia.

,, 3. ,, 3 undivided cells, 1 antheridium.

,, 4. ,, 1 undivided cell, 1 dividing into an antheridium, 2 antheridia.

,, 5. ,, 3 antheridia, one 16-celled colony.

,, 6. ,, no antheridia, four 16-celled colonies.

(*b*) Male colonies (when the cells were in the early stages of division, it was not possible to judge whether they would have become antheridia or daughter-colonies, but all the data below were obtained from collections containing colonies with ripe sexual cells and devoid of normal asexual colonies).

Specimen 1. 1st tier 2 in 4-celled stage, 2 in 8-celled stage.

2nd ,, 6 antheridia, 2 in 8-celled stage.

3rd ,, 7 antheridia, 1 in 16-celled stage.

4th ,, 8 antheridia.

5th ,, 4 antheridia.

,, 2. 1st ,, 4 undivided.

2nd ,, 1 undivided, 1 degenerate, 6 in 16-celled stage.

3rd ,, 7 in 16-celled stage, 1 degenerate.

4th ,, 8 in 16-celled stage.

5th ,, 3 in 16-celled stage, 1 degenerate.

,, 3. 1st ,, 4 undivided.

2nd ,, 1 in 2-celled stage, 2 undivided, 1 in 4-celled stage, 4 in 8-celled stage.

3rd ,, 1 in 4-cel'ed stage, 3 in 8-celled stage, 4 in 16-celled stage.

4th ,, 8 in 16-celled stage.

5th ,, 4 in 16-celled stage.

Specimen 4. 1st tier 4 undivided.
         2nd ,, 8 antheridia.
         3rd ,, 8 antheridia.
         4th ,, 8 antheridia.
         5th ,, 4 antheridia.

The sexual cells resembled those of *E. elegans*, and the spermatozoids were seen swarming round the egg-cells, though actual fertilisation was not observed.

Since Kofoid described his *Pleodorina illinoisensis*, repeated doubts have been expressed as to the validity of the species. While some have accepted it with a measure of suspicion, others have expressed the view that it should be regarded as a *Pleodorina*-state of *Eudorina elegans*. Grove suggested that the species was not yet fixed, being still in process of evolution. All previous workers, however, have regarded *E. illinoisensis* as essentially characterised by the somatic nature of the front four cells and have found this not to be universal. For, while sometimes they are truly somatic, they are mostly capable of division. But, though the species appears ill circumscribed when tested from this point of view, it shows a very definite character of its own, when its reproductive vagaries are carefully analysed.

This character, which gives it a distinct specific and perhaps even a generic status, is afforded by the markedly different behaviour of the front four cells in every colony, as compared with that of the remainder. Thus, (1) when the rear cells become oogonia, the front cells become antheridia ; (2) when the rear cells become oogonia, or full-sized thirty-two celled coenobia, the front cells become either antheridia or form small-sized sixteen-celled coenobia ; or, (3) when the rear cells form antheridia, the front cells fail to divide or divide at a late stage into a few cells. The behaviour of the front four cells is always quite distinct from that of the remainder and *on this basis* this form can be established as a distinct species. ˙A tendency in this direction is observable even in *E. elegans* (cf. p. 333, and Pascher, 1927, p. 437).

Grove found that starving the colonies by cultivating them in distilled water induced the formation of numerous antheridia. This perhaps indicates that, when accumulation of food is prevented or vitality lowered, development of oogonia is prevented. Looked at from this point of view, it may be said that the behaviour of the front four cells of the *E. illinoisensis* colony in nature is in every instance one step, as it were, behind that of the remainder. They do not appear to possess the same reproductive efficiency. It is conceivable that they are so specialised, in relation to light-perception and the work of steering the colony, that their vitality for reproductive purposes has become lessened, so that, as compared with *E. elegans*, in which every cell is capable of developing into an oogonium or full-sized colony, these cells have lost part of their reproductive capacities.

The diagnosis of *Eudorina illinoisensis* should, therefore, be modified to read as follows :—

Colony of thirty-two or often sixteen cells, resembling *Eudorina elegans*

Ehrenb., but the front four cells smaller (in a greater or lesser degree) than the remaining ones, and either purely somatic or reproducing differently from the remaining cells of the same colony.

Much of the present uncertainty as regards the specific status of *Pleodorina illinoisensis* is due to Kofoid's description of the species being based on specimens whose full life-history he was not able to follow owing to the short period during which they were available. If he had seen the reproductive stages that have since been recorded, he would not have assumed that the front four cells were invariably purely somatic. The few divisions of the front cells that he did observe, he evidently regarded as aberrant or as exceptions to the general rule. So far as I am aware, no forms have subsequently been recorded answering strictly to the letter of Kofoid's definition of *Pleodorina illinoisensis*.

Pascher has included this alga under *Eudorina* as *E. illinoisensis*, because the front four cells are capable of division and because the cells are arranged in tiers as in *E. elegans*. Its removal from *Pleodorina* is certainly justified, but *E. illinoisensis* cannot be regarded as conforming, in the strictest sense, to the past definition of *Eudorina*, since in some male colonies the four front cells (or some of them) are truly somatic and do not divide. Moreover, while in *Eudorina* proper every cell in the female colony can become an oogonium, the front four cells of *E. illinoisensis* cannot develop into oogonia. Pascher (1927, pp. 439, 443) has consequently given an emended diagnosis of *Eudorina* to embrace Kofoid's *Pleodorina illinoisensis*. *E. illinoisensis* possibly exhibits a step in the direction of *Pleodorina*.

Dimensions of the Indian material :—

Thirty-two-celled colony 110–140 μ long and 95–118 μ broad (110×95 μ, 120×100 μ, 120×95 μ, 128×102 μ, 138×101 μ, 130×109 μ, 110×100 μ, 130×104 μ, 132×110 μ, 140×112 μ, 140×110 μ, 140×120 μ). Sixteen-celled full-grown colony 96×71 μ. Sixteen-celled young colony 55×30 μ.

The dimensions of the cells are given on p. 336.

EUDORINA INDICA, sp. n. (Text-fig. 3 ; Pl. **28.** figs. 2, 12, 13.)

This alga was first collected by Dr. Sampathkumaran in a rain-water pool at Talguppa in Mysore Province, and subsequently by me in a similar pool at Madras. The colonies contained sixty-four cells which were arranged in seven tiers of 4, 8, 12, 12, 12, 12, and 4 cells respectively, from the anterior to the posterior end (text-fig. 3, A, B). The colony was ellipsoidal to subglobose, and the cells were similar to those of *Eudorina elegans* in shape. The cells of the first four-celled and second eight-celled tiers were decidedly smaller than the remainder, although those of the second tier were larger than those of the first. In the following four twelve-celled tiers, composed of relatively larger cells, there was a gradual though slight increase in size in passing from the anterior to the posterior end. The posterior tier of four cells, however, was an exception to this rule, the cells being slightly smaller than those of the

TEXT-FIG. 3.
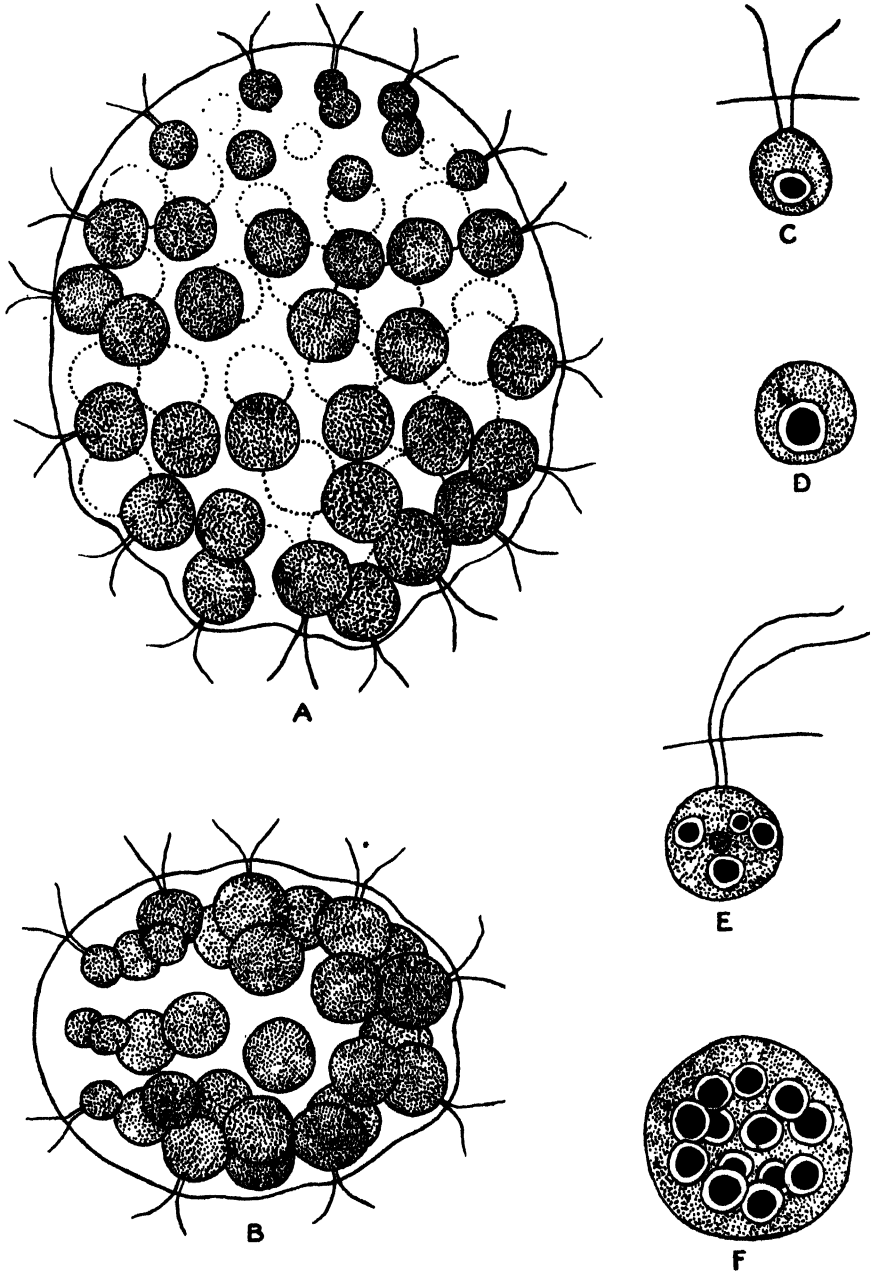
Eudorina indica, sp. n.

A, 64-, and B, 32-celled colonies; C, an anterior, and D, a posterior, cell from a young
colony; E, F, the same from a mature colony. Pyrenoids black,
(A & B, ×400; C–F, ×1225.)

penultimate tier. In illustration of this the dimensions of two colonies are given (in μ) :—

(1) Full-grown ellipsoidal colony, 175×131.
    Cells of the 1st tier 8·75–12.
       ,,   ,,   2nd tier 12–14.
       ,,   ,,   3rd–6th tier 16–23·5.
       ,,   ,,   7th tier 20.
(2) Smaller colony, 140×110.
    Cells of the 1st tier 10.
       ,,   ,,   2nd ,, 10–12·5.
       ,,   ,,   3rd ,, 14–16.
       ,,   ,,   4th–6th tiers 16–17·5.
       ,,   ,,   7th tier 17.

As in other cases, the eye-spots of the first tier are the largest and those of the succeeding tiers are progressively smaller, the posterior tier having extremely minute eye-spots or none whatever. Each cell has more than one pyrenoid when fully grown, but the cells of the two front tiers contain only a few pyrenoids, while those of the remaining tiers have up to sixteen pyrenoids (text-fig. 5, E, F). The following are the numbers of pyrenoids in the cells of a single full-grown colony :—

    1st and 2nd tiers . . . .   3 pyrenoids in each cell.
    3rd tier . . . .   8–10 pyrenoids in each cell.
    4th–7th tier . . . .   12–16 pyrenoids in each cell.

The posterior cells in full-grown colonies are generally crowded with pyrenoids.

The colonies, when young, have all the cells nearly of the same size, each with one pyrenoid (text-fig. 3, C, D). As the colony grows larger, all the cells increase in size equally for a time, and the number of pyrenoids increases by new ones arising *de novo*. After a certain stage is reached, the cells of the first tier undergo no further increase in size and no further pyrenoids are formed in them, and soon after the same thing happens with respect to the second tier of cells. Increase in size and formation of additional pyrenoids continue, however, in the cells of the remaining tiers for some time.

Only one colony was observed in which the cells were undergoing division (Pl. 28. fig. 2). The twelve anterior cells, belonging to the first and second tiers, were not dividing. Of the twelve cells of the third tier, three were not dividing, one had divided into two, another into four, and another into eight cells. The remaining cells of this tier and all the cells of the two immediately following were dividing to form daughter-coenobia, whilst those nearest the posterior end were forming antheridia. The antheridia usually had thirty-two spermatozoids in the bundle, although one bundle contained only sixteen cells. No other reproductive stages were observed in the material.

This alga is more advanced than *E. illinoisensis*, and in some respects stands between it and *Pleodorina californica*. Unfortunately, little is known about
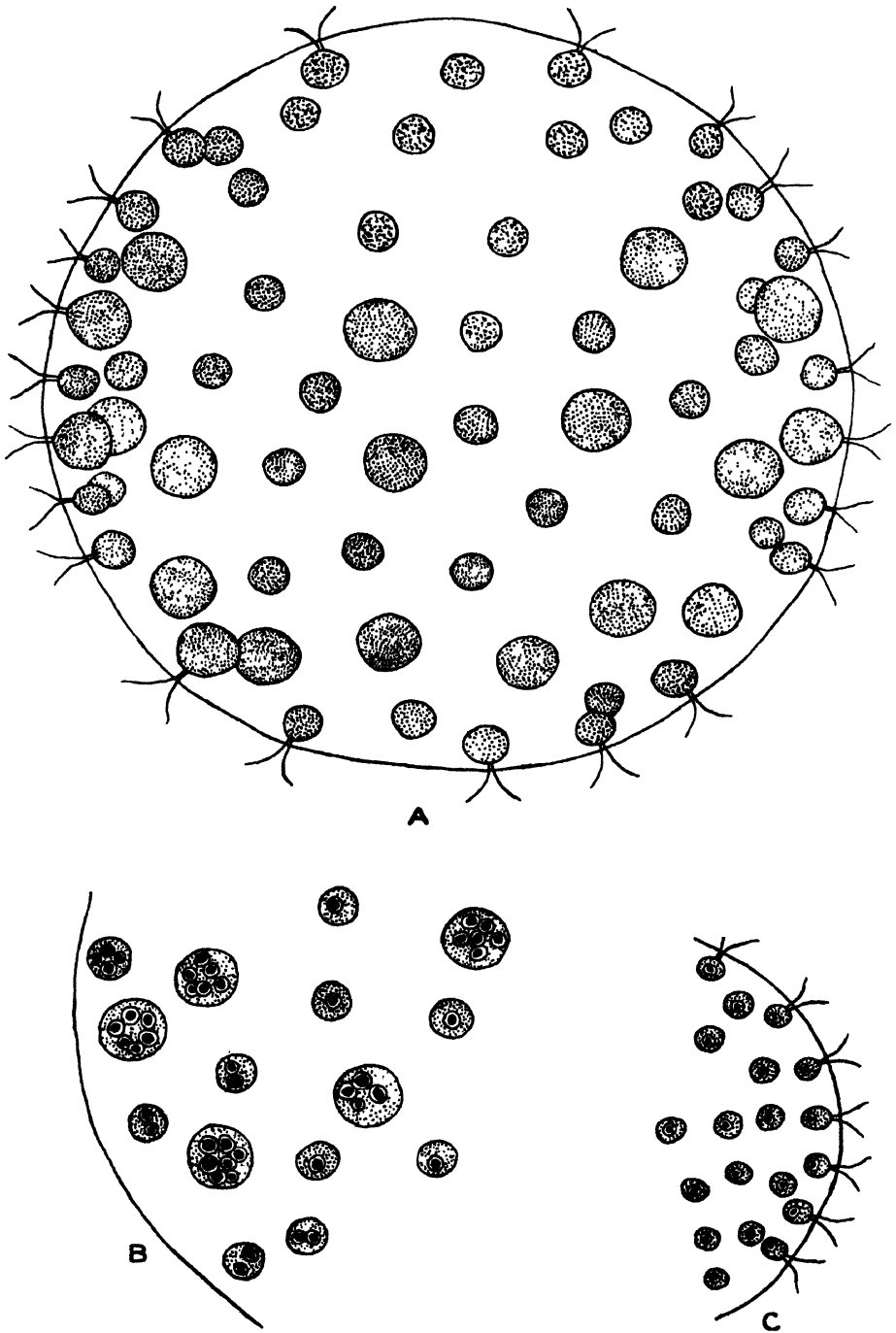
Pleodorina sphaerica, sp. n.

A, a mature colony ; B, portion of a mature colony with gonidia and somatic cells ;
C, portion of a young colony. Pyrenoids black. (All × 495.)

its reproduction, but the one case observed indicates that the front twelve cells do not divide, while most of the others do so. It is possible that in this alga the front twelve cells are truly somatic.

In the same collection were a number of colonies having thirty-two cells and resembling those of *E. illinoisensis* (Pl. **28**. fig. 13 ; text-fig. 3, B), but the cells of the front two tiers were smaller than those of the remainder, and those of the first tier were smaller than those of the second. These are evidently smaller (thirty-two-celled) colonies of *E. indica*.

PLEODORINA SPHAERICA, sp. n.   (Text-fig. 4 ; Pl. **28**. figs. 4, 5.)

This new species of *Pleodorina* was found sparsely scattered among other algae in a pool on a hill-slope at Vandalur near Madras. The alga is of special interest in having numerous gonidial cells interspersed among somatic cells.

The colony is spherical or nearly spherical, and contains 128 cells, which are arranged in no special manner near the periphery. The full-grown colony measures 187–210 μ in diameter. One part of the colony, presumably the anterior portion, forming about one-fourth to one-fifth of the whole, is free from gonidia. In the remaining part a large number of gonidia are found scattered among somatic cells (text-fig. 4, A, B ; Pl. **28**. figs. 4, 5). The somatic cells measure about 9–11 μ and the gonidial cells 15–17 μ in diameter. The detailed structure of the cells was that typical of *Eudorina* and *Pleodorina*. Eye-spots could not be detected in the preserved material.

The cells of the young colonies are all equal in size and contain a single pyrenoid (text-fig. 4, C), and all the cells exhibit uniform increase in size up to a certain stage. Then the somatic cells cease to grow, and only those continue to enlarge which are to become gonidia. In these cells further pyrenoids are formed, while in the somatic cells there is no increase in the number of pyrenoids or only ône or two additional ones are formed. In the full-grown colonies the number of pyrenoids in the somatic cells is one to two, sometimes three, while in the gonidial cells there are six to eight pyrenoids (text-fig. 4, B). Unfortunately, no division-stages were found in the material, and, although the pool was searched during the next two years, the alga was not found again.

This alga, in the irregular disposition of its cells and the limited number of gonidia, is clearly allied to *Pleodorina californica* Shaw (1894, pp. 279–283), but appears to be more advanced. In *Eudorina illinoisensis* the front four cells show signs of becoming somatic. In *E. indica*, where the colony is slightly larger, a bigger proportion of the cells (i.e. twelve out of sixty-four) become somatic. In *Pleodorina californica* there is still further advance, not only in the size of the colony and the number of its cells, but also in the fact that nearly half the total number of cells are somatic. In actual fact practically the whole anterior half of the colony is somatic, while the posterior half is gonidial. In the present alga, while a small area of the anterior portion is again somatic as in *P. californica*, a still further advance is indicated by the fact that a large number of the posterior cells have become somatic. In other

words, the process of sterilisation has invaded even the posterior region, which in *Eudorina illinoisensis*, *E. indica*, and *Pleodorina californica* is purely gonidial. In fact, *P. sphaerica* shows a condition very closely approaching that of *Volvox*, where usually a relatively small number of gonidial cells are found scattered among the somatic cells in the posterior region of the colony. But for the limited number of cells, this alga might be classed under *Volvox*.

The evolution of certain *Volvox*-forms from a *Pleodorina*-like ancestor, especially from a form like *P. californica*, is probable. *P. sphaerica* is of interest in this connection in providing yet another important link, showing how sterilisation has invaded even the purely gonidial posterior region of a *P. californica*, and has thus brought about a condition similar to that of *Volvox*.

The alga here described has a definite number of cells, and the gonidial cells are scattered among the somatic cells. There are no protoplasmic connections. It could thus be placed under *Besseyosphaera*, as Shaw (1916, pp. 253–4) defines this genus. But *Besseyosphaera* is akin to *Volvox*, if not a *Volvox* itself, being a large form with about a thousand cells, while the present alga with its small size and limited number of cells falls naturally into the series *Gonium* (4, 8, 16 cells), *Pandorina* (8, 16, 32 cells), *Eudorina* (8, 16, 32, 64 cells), and *Pleodorina* (64, 128 cells). There is still a big gap between *Pleodorina* with the limited number of cells and even the smallest species of *Volvox* with numerous cells. I am therefore of the opinion that the alga should be included in *Pleodorina*, though this will necessitate a slight modification of the present diagnosis of the genus.

The progressive series of forms discussed in the preceding pages may be summarised as follows :—

(1) *Pandorina morum* (8- and 16-celled solid colonies ; cells with a single pyrenoid).

(2) *Pandorina morum* f. *major* (8–16- and 32-celled solid colonies ; cells with many pyrenoids).

(3) *Eudorina elegans* (16- and 32-celled hollow colonies, with cells placed peripherally ; cells with many pyrenoids).

(4) *Eudorina illinoisensis* (16- and 32-celled hollow colonies ; front 4 cells progressing towards sterilisation).

(5) *Eudorina indica* (32- and 64-celled hollow colonies ; front 12 cells somatic).

(6) *Pleodorina californica* (64- and 128-celled hollow colonies ; cells of front half somatic, remainder gonidial).

(7) *Pleodorina sphaerica* (128-celled hollow colony ; as in *P. californica*, but many cells even in the posterior region somatic).

(8) *Volvox* (colony very large and composed of numerous cells ; somatic cells very numerous as compared with the gonidia).

VOLVOX PROLIFICUS, sp. n.   (Text-fig. 5, A–G ; text-fig. 7, J ; text-fig. 8, A ; text-fig. 9, C ; Pl. 28. figs. 3, 6, 9, 20, 23.)

This species was collected by Mr. M. S. Raghava Chari in a pool in the bed of the river Nagari, near Tirupati in South India.   The pool was on the point

of drying up, but at the time of collection the alga occurred in such enormous numbers as to make the water appear bright green, even from a distance.

The colonies of *V. prolificus* are either asexual or sexual, the sexual colonies being in the main dioecious. The asexual and female colonies are globose or subglobose, while the male are subglobose to ellipsoidal. The female colonies are slightly broadened at the anterior and somewhat narrowed at the posterior end (Pl. 28. fig. 3). Often a few (two to five) daughter-individuals are seen in a male or female colony. A single asexual colony was found to contain a number of well-developed oogonia and oospores, and one very old male colony contained a single ripe oospore. The number of cells in the colony is 9,000 to 25,000. The asexual colonies measure from 400 to 1010 μ in diameter, the female from 400 to 1090 μ, and the male from 410 to 800 μ.

In surface-view the boundaries of the cells are pentagonal or hexagonal in outline (text-fig. 5, A). In optical section they are found to be about 30 μ deep with parallel sides. The protoplasts of the colony thus lie between two curved contours representing the outer surface of the colony and the slightly curved inner surfaces of the cells bounding the large central hollow. The cells possess much the same structure as those of *V. globator* (Meyer, 1896, pp. 187–217). There are usually five protoplasmic connections, often there are four, and occasionally six (text-fig. 5, A ; text-fig. 8, A). In an optical section of the colony they are seen to arise from the sides of the protoplast and to spread out horizontally, but in a slightly downward direction (text-fig. 5, B). In younger colonies the main body of the protoplast is rounded in surface-view and pear-shaped in side-view, with the pointed end directed outwards. In the older colonies, however, it appears irregularly rounded in surface-view and narrowly pear-shaped or wedge-shaped in side-view (text-fig. 5, B, D). The cilia, especially in the wedge-shaped cells, are placed well apart from each other.

In very old colonies of *V. prolificus* the protoplasmic connections disappear and the protoplasts constitute rounded masses in the centre of the cells, while the thick gelatinous walls appear about to disorganise. In such old colonies one sees, in surface-view at a high focus, internal to the polygonal boundary-walls, a second closely apposed membrane which has a rounded outline and is readily distinguishable only at the corners (text-fig. 5, E, F). In optical section this second membrane appears rounded on the outer surface, so as to leave a small space between it and the bounding membrane on either side or more frequently on one side only (text-fig. 5, G).

The protoplasts are more densely crowded on the posterior than on the anterior side of the colony, the distance between them at the posterior and anterior ends being 1·5 μ and 2–3 μ respectively. The protoplasts are 5–6 μ in diameter, and, in the preserved material, appear sometimes slightly larger in the young than in the full-grown colonies. The protoplast contains a somewhat bell-shaped chloroplast in which is embedded a single pyrenoid. The single nucleus is situated in the centre of the protoplast within the cup-shaped hollow of the chloroplast (text-fig. 5, D).
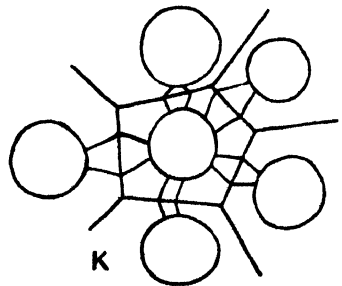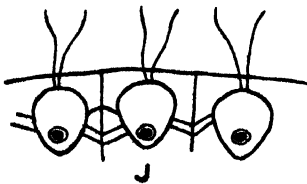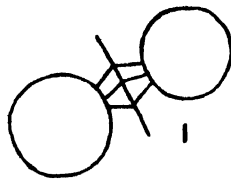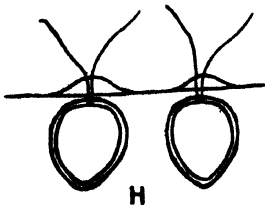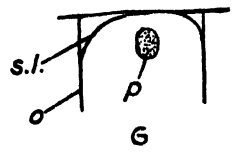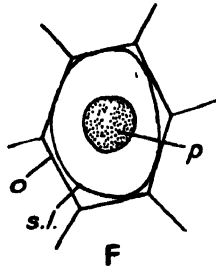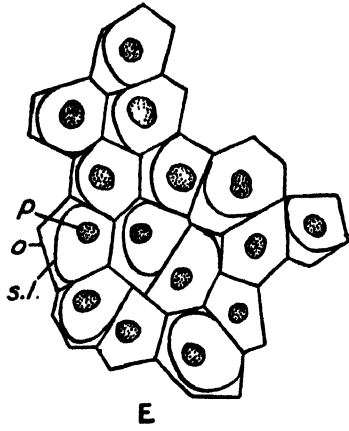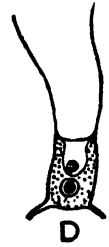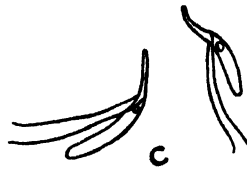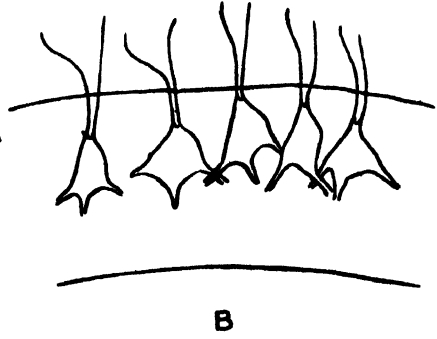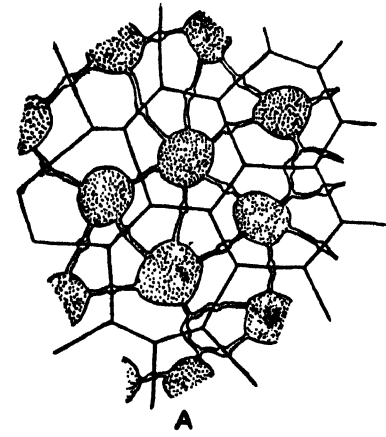
EXPLANATION OF TEXT-FIG. 5.

A–G. *Volvox prolificus*, sp. n.

A, surface-view ; B, optical section showing the form of protoplasts ; C, spermatozoids ; D, single cell with chloroplast, pyrenoid, and nucleus ; E, surface-view of cells from a very old colony ; F, a single cell of E enlarged ; G, optical section of the upper portion of a cell of E (diagrammatic). *p*, protoplast ; *o*, outer layer of cell ; *s.l.*, second layer of wall.

H–K. *V. dissipatrix* (Shaw), comb. nov.

H, cells showing protrusion of the gelatinous layer ; I, and K, protoplasmic connections between cells in surface-view ; J, the same in optical section.

(A, C, F, H, K, × 1200 ; D, E, × 640 ; B, × 810 ; I, × 1950 ; J, × 975.)

V. prolificus differs from all hitherto-described species of *Volvox* in the fact that the reproductive cells are differentiated continuously throughout the existence of the colony.* In fact, most of the cells appear to retain the capacity to take on reproductive functions at any stage in the life of the colony, whereas in the other species of the genus, once the gonidia or sexual cells are differentiated the other cells remain definitely somatic. The reproductive cells are, however, restricted to the posterior half of the colony in the manner customary in *Volvox*.

Asexual colonies.—The continuous differentiation of reproductive cells is not so noticeable in the asexual as in the sexual colonies, owing to the relatively small number of gonidia formed. Side by side with developing daughter-coenobia, however, one always finds a small number of enlarging cells, which are growing into further gonidia. In very old colonies containing a considerable number of daughter-coenobia, moreover, the latter are usually of very different sizes, some being very much smaller than others and comprising a much smaller number of cells (text-fig. 7, J). The difference in size and cell-number is evidently due to their successive formation. The total number of daughter-coenobia formed varies between four and twenty, the usual number being six to twelve. Very young coenobia are not completely spherical, but slightly ellipsoidal. At the time of birth they measure about 153–230 μ in diameter. The gonidia commence to differentiate before the birth of the colony.

Male colonies.—Formation of antheridia begins in very young male colonies which are of small size, and more and more antheridia are produced throughout life, so that in the older and larger male colonies one finds antheridia in all, from the earliest to the latest, stages of development. In a young colony one finds antheridia with spermatozoids ready to escape, and a certain number of developing antheridia scattered over the posterior half. In slightly older colonies there are maturing antheridia and a number of spaces representing the

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* In the male colonies of some species (*V. perglobator* Powers and *V. Rousseleti* West var. *lucknowensis*, cf. p. 350) there is a successive formation of antheridia, though not as marked as in *V. prolificus*.
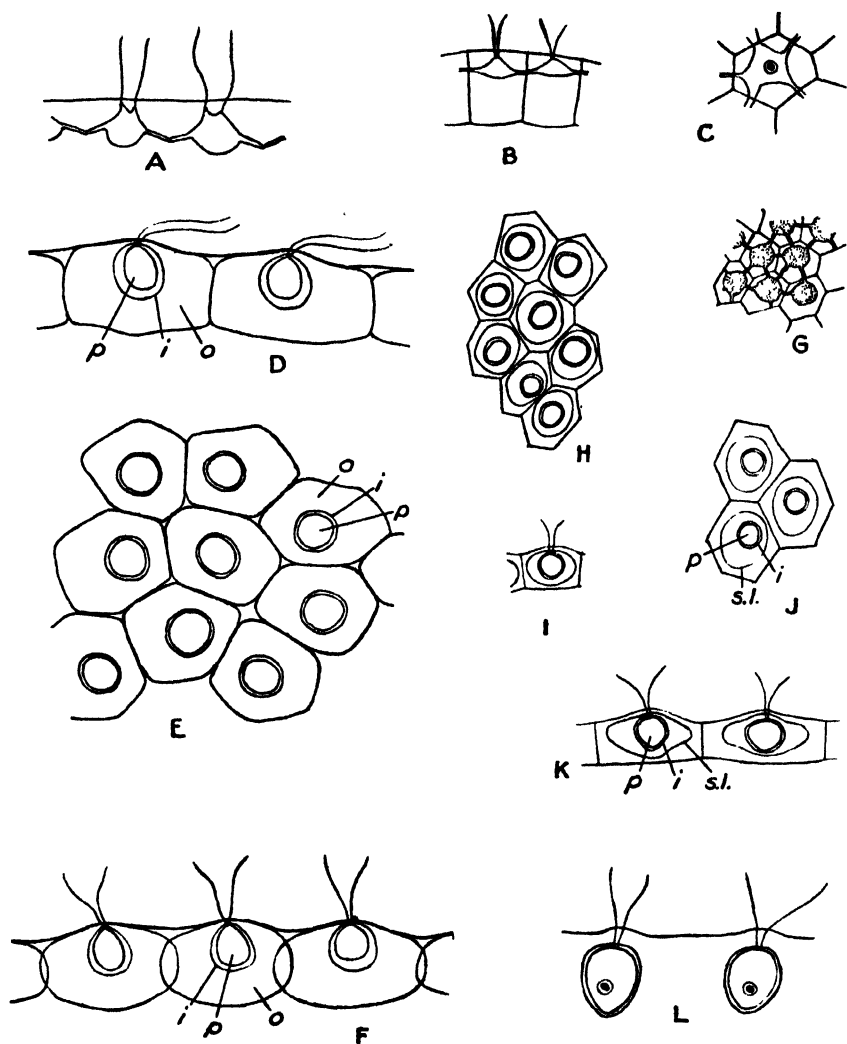
Cell-structure in species of *Volvox*.

A–C. *Volvox globator* Ehrenberg var. *maderaspatensis*, nov.

A, cells in optical section.   B, the same, showing the limits of the cell-membranes.   C, cell in surface-view.

D–F. *V. Carteri* Stein.

D, cells in optical section showing limits of walls;   E, cells in surface-view;   F, optical section of cells from a very old colony.

G, *V. Rousseleti* West var. *lucknowensis*, nov., cells in surface-view.

H, *V. africanus* West, surface-view of cells drawn from Shaw's material.

I–L. *V. africanus* West f. *minor*, nov.

I, cell in optical section from the posterior end of a young colony;   J, surface-view of cells from the anterior end of an older colony;   K, optical section of cells in the anterior end of an older colony;   L, cells showing the protrusion of the gelatinous envelope opposite the protoplasts.

(A–F, L, × 915;   G–J, × 480;   K, × 765.)

empty antheridia from which the spermatozoid bundles have escaped ; at the same time there are again a number of cells in the early stages of antheridium-formation. The same state of affairs is met with even in very old colonies about to disintegrate. There can therefore be no doubt that successive crops of antheridia are formed in this species of *Volvox*. The number of antheridia in young colonies is small (up to twenty-five) ; in the older colonies more numerous antheridia (up to fifty-five) are observed, quite apart from those which have already liberated their spermatozoids and are no longer clearly recognisable.

The antheridia are round and disc-shaped, from 38 to 40 μ in diameter, and form numerous (about 256) spermatozoids arranged in, a single layer (Pl. **28.** fig. 20). The male cells, so far as could be ascertained in preserved• material, are narrow, elongate, spindle-shaped structures, about 13–15 μ long and about 0·9 μ broad. The cilia are attached at a certain distance from the anterior end, the part of the body in front of their point of attachment being narrowed into a beak. Below the point of insertion there is a round space, evidently a contractile vacuole (text-fig. 5, C).

Female colonies.—The oogonia are about 80–150 in number in young colonies and gradually increase in number as the colonies grow older and larger, reaching 500 or more in the fully developed colonies. In the young female colonies a quantity of mature oogonia are found, as well as a number of enlarging cells scattered over the posterior half which no doubt represent developing oogonia. In older colonies, and even in such as are breaking up, oogonia in various stages of development are still to be found side by side with others containing ripe oospores.

Very young female colonies, however, appear to be bisexual, for every such colony had two to six spaces in it which evidently represent the positions occupied by antheridia from which the spermatozoids have escaped ; a few spermatozoids are, in fact, often still to be seen in these spaces. Numerous young colonies, including daughter-colonies inside the mother, have been carefully examined, but actual antheridia could not be found in any of them. In several ·young female colonies, however, division-stages of enlarged cells have been observed, but whether these would have given rise to antheridia or merely to daughter-coenobia it is impossible to say. The number of such dividing cells was two to six, i.e. equal to the number of presumed antheridia, and it is therefore probable that they represent the developing antheridia.

The ripe oospore has two walls—the inner smooth, the outer spinous. The spines are strong and conical (5–7 μ long), with a fairly broad base. In median optical section fourteen to sixteen spines are visible around the periphery of the spore. Without the spines the oospores measure 30–35 μ in diameter (text-fig. 9, C ; Pl. **28.** fig. 23). The spines are fully developed only in ripe spores, the younger ones having blunter and shorter spines, while in the earliest stages the spore has a crenate or even a smooth wall. All these stages can be seen in one and the same colony.

Development of reproductive cells.—As the cells enlarge to form gonidia, antheridia, or oogonia, they gradually project into the central hollow of the coenobium and ultimately come to lie below the general surface, although the outer portion of their gelatinous wall still occupies its former position between the other cells of the colony. This is as in other species. There is no rupture of the general surface at these points. In this species the protoplasts of the reproductive cells, however, are surrounded by a very wide mucilaginous envelope, formed from the original gelatinous wall by enlargement and several times exceeding the protoplasts in width. The large mucilage-envelope surrounding them is readily stained with alcoholic safranin, or dilute aqueous methylene or toluidine blue. When these reproductive cells are remote from each other, the envelopes appear as rounded vesicles, but when they are closely crowded the envelopes become angular through mutual pressure, and on staining appear like internal reticulations. This is best seen in a well-developed female colony with numerous oogonia (Pl. 28. fig. 9).

In old colonies about to disintegrate, the gelatinous envelopes of the somatic cells become diffluent, and appear as a broad transparent layer of homogeneous mucilage which reaches far into the interior of the colony. This is very clearly seen in the asexual colonies in which the daughter-coenobia, with their own individual gelatinous envelope still intact, lie in the broad homogeneous mucilage derived from the gelatinous envelopes of the somatic cells.

VOLVOX ROUSSELETI West var. LUCKNOWENSIS, nov. (Text-fig. 6, G ; text-fig. 7, F ; text-fig. 8, B ; text-fig. 9, G ; Pl. 28. figs. 8, 11.)

I am indebted to Prof. Fritsch for placing this material at my disposal. It was collected by Mr. A. R. Roa in Lucknow in 1929, but no further information about the habitat is available.

The colonies are subglobose to ellipsoid, and measure 510–629×544–765 μ (510×544 μ, 510×612 μ, 527×561 μ, 544×595 μ, 629×765 μ, 697×731 μ, 697×765 μ) ; they contain 6,000 to 8,000 cells. They are either asexual, male or female, female colonies being present in the largest numbers. Up to ten spaces can be seen in the asexual and female colonies, so that the very young coenobia of these types contain a few antheridia. A few gonidia or daughter-coenobia (up to five) are sometimes seen in the antheridial or female colonies.

The protoplasts are rounded to somewhat broadly stellate in surface-view (text-fig. 8, B), and measure 5·5–7·5 μ in diameter. The protoplasmic connections are thin, but not delicate ; they were often disintegrating all over the colony. In an optical median section of the colony the protoplasmic connections appear to arise a little below the middle of the protoplast. The actual outline of the cells is hexagonal or pentagonal in surface-view (text-fig. 6, G) and rectangular in side-view. The height of the cell (equivalent to the thickness of the gelatinous matrix of the coenobium) is 25–29 μ. The distance between the centres of adjacent cells at the anterior and posterior ends of one colony were 13 μ and 9·5 μ respectively.

Asexual colonies.—Three to seven gonidia may be seen in the asexual colonies, some being larger than the others. The larger ones are nearer the middle and the smaller nearer the posterior end of the colony (text-fig. 7, F).

Female colonies.—These are slightly narrowed towards the posterior and broadly rounded at the anterior end (Pl. 28. fig. 8). The number of oogonia varies between 100 and 159, and they are found throughout the colony except for about the anterior fifth. The oospore has an inner smooth and an outer spinous wall. The spines are normally rather short and broadly conical (text-fig. 9, G), but all gradations from oospores with a truly crenate wall to such as bear broadly conical spines are seen in the same coenobium. The crenate walls do not, however, appear to belong to spores which are immature. Thus, in one specimen, the spores with crenate walls had already formed the inner (smooth) layer, while those with spinous walls had not yet formed this layer. The former were evidently the older. The spiny oospores are 32–33·5 μ wide without the spines, the spines being 3·7–5·5 μ long. The crenate oospores measure 33–35 μ in diameter.

Male colonies.—The male colonies form from twenty to sixty antheridia, which are about 40 μ in diameter. The antheridia produce sperm-globoids, which are at first spherical, but become flattened when fully grown, measuring about 19×40 μ. The number of spermatozoids appears to be 256. No free spermatozoids were seen in the material. The antheridia are found in all stages of development in the male colonies, from the just enlarging somatic cell to the large undivided antheridium and from this in all stages of division to the fully formed sperm globoid (Pl. 28. fig. 11). Such a condition has been reported by Powers (1908, p. 164) as occurring frequently in *V. perglobator*.

The female colonies resemble those of *V. Rousseleti* West (1918, pp. 425–8, pls. 29 & 30) in their general shape, and there is also similarity in the cells and protoplasmic connections, as well as in the dioecious habit. The colonies, however, are not so large as those of *V. Rousseleti*, and consist of a smaller number of cells. Moreover, the spines on the oospores are not at all like those of *V. Rousseleti*, but resemble more those of *V. globator* in being short and broadly conical. In the presence of a number of crenate oospores, in the antheridia being found in all stages of development, and in the dioecious nature of the colonies, it comes near to *V. perglobator* Powers, but it differs from this species in the frequent spiny walls of the oospores and in the rather different type of cell-structure which Powers describes for his species.

The form under discussion, therefore, combines characters of both *V. perglobator* and *V. Rousseleti*, but it appears to stand closer to the latter and may for the present be described as a new variety of *V. Rousseleti* under the name of var. *lucknowensis*.

VOLVOX GLOBATOR Ehrenberg var. MADERASPATENSIS, nov. (Text-fig. 6, A–C; text-fig. 7, G; text-fig. 8, C; text-fig. 9, A; Pl. 28. figs. 10, 15, 24.)

This alga was collected by Dr. T. Ekambaram in a pool inside a *Casuarina*-plantation near Elliot Beach in Madras during the winter monsoon season
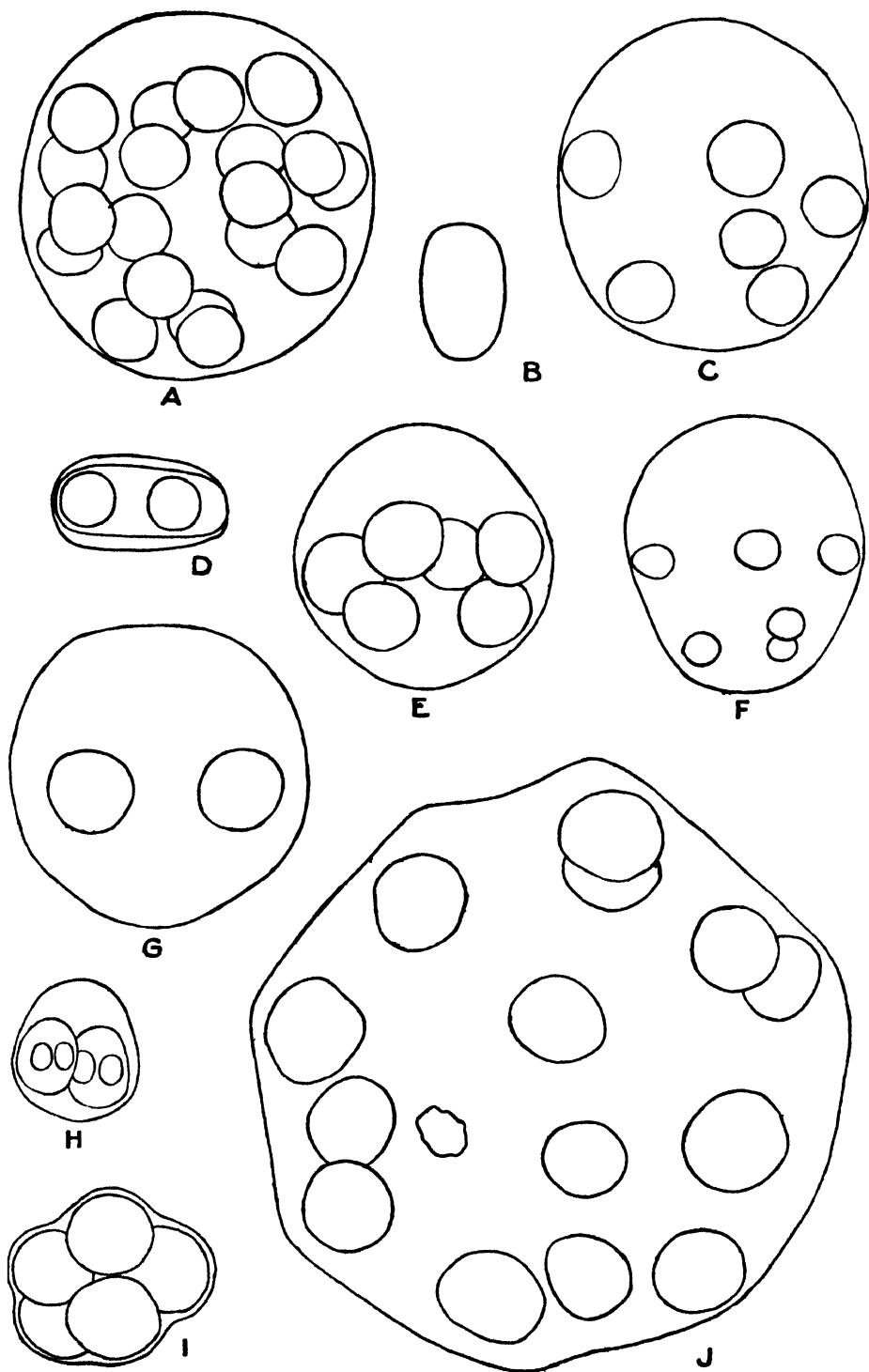
EXPLANATION OF TEXT-FIG. 7.

Asexual colonies and disposition of daughter-coenobia in species of *Volvox*.

A, *V. Carteri* Stein f. *nagariensis*, nov.; B, *V. africanus* West f. *minor*, nov. (side-view);
C, *V. dissipatrix* (Shaw), comb. nov.; D, *V. africanus* West f. *minor*, nov. (view from
anterior end); E, *V. Carteri* Stein; F, *V. Rousseleti* West var. *lucknowensis*, nov.;
G, *V. globator* Ehrenberg var. *maderaspatensis*, nov.; H, *V. africanus* West f. *minor*,
nov.; I, *V. Merrilli* Shaw f. (?); J, *V. prolificus*, sp. n.   (A–H, *J*, × 60; I, × 48.)

of 1930. It occurred sufficiently abundantly to give the water a green
colour.

The asexual coenobia were subglobose, while the sexual ones were elliptic
to elliptic-obovate, being slightly broader at the posterior than at the anterior
end. The asexual colonies attained to 693 μ in diameter, while the sexual
ones measured as much as 640×759 μ. The protoplasts were 5·5–7·5 μ in
diameter; they were somewhat rounded when young, though later becoming
angular where the protoplasmic connections arose and often appeared quite
stellate. In optical section they were more or less rounded, though horizontally
extended (text-fig. 6, A, B). The protoplasmic connections were often long
and thin, but not very fine. The boundary of the cell-wall was pentagonal
or often hexagonal in surface-view and rectangular in side-view (text-fig. 6, C, B).
The number of cells in the colony was 6,000 to 11,000.

The asexual coenobia generally produced only two to four gonidia, usually
only two (text-fig. 7, G), which were placed on opposite sides in the median
portion of the coenobium, a little towards the posterior end. They are not
differentiated in the young coenobia, which reach about 180–204 μ in diameter
before birth.

The sexual coenobia (Pl. **28**. fig. 15) were monoecious and protandrous.
They contained seven or eight antheridia, but only a few specimens in the
material showed them, their former position in most of the colonies being
represented by spaces. The oogonia were 18–38 in number and were as usual
confined to the posterior portion, the front two-fifths of the coenobium generally
not containing any. The oospores differed from those of the type in being
clothed with strong, sharp, conical spines; which were 8–13 μ long and often
slightly curved at the tip, the curvature not always being in the same direction.
The inner layer of the membrane was smooth (text-fig. 9, A; Pl. **28**. fig. 24).
The oospores were 35–42 μ in diameter without the spines, fourteen to fifteen
spines being visible around the periphery, when viewed in optical section.

This alga forms a link between *V. globator* and *V. Merrilli* Shaw. In the
small number of antheridia and oogonia it resembles *V. globator*, but in the
character of the protoplasts, with the often long and moderately thin proto-
plasmic connections, in the long sharp spines of its oospores, and in the smaller
size of the latter, it resembles *V. Merrilli*. The very small number of gonidia
and their arrangement are features peculiar to the form under discussion.
It may be seen from the above that it might be regarded as a variety of *V. globator*
from one point of view and of *V. Merrilli* from another. Since it thus combines

the characters of both species and presents some peculiarities of its own, it might be justifiable to regard it as a distinct species. But the small number of its antheridia and oogonia, and the general appearance of its colonies incline me to rank it as a variety of *V. globator*, which I shall call var. *maderaspatensis*. Some of the existing species of *Volvox* with protoplasmic connections may, as more information about them becomes available, prove to be only varieties of *V. globator*.

VOLVOX MERRILLI Shaw (1922, pp. 492–496), forma (?). (Text-fig. 7 ; text-fig. 8, D ; text-fig. 9, F.)

This form was found in a pool in a *Casuarina*-plantation near the sea-coast at Seven Pagodas, near Madras. The pool was somewhat shaded by the trees, and only a small amount of direct sun-light reached the water. The alga occurred very sparsely and was collected by pouring the water through a broad funnel covered with bolting silk. The material thus obtained proved to be very old and in a very poor condition, most of the colonies being much shrivelled and about to disintegrate. Only a few colonies were found in which the details could be made out.

Only asexual colonies with fully developed daughter-coenobia and female colonies with ripe oospores were present. The former were globose to sub-globose, while the sexual colonies were ellipsoid. The asexual colonies measured 495–750 μ in diameter, while the sexual colonies were 412–500×580–660 μ (412×580 μ, 490×590 μ, 500×660 μ). The number of cells, as far as could be recognised in the poor material, was 5,000 to 11,000.

The protoplasts, as seen in surface-view, were round when young, but gradually became angular opposite the protoplasmic connections (text-fig. 8, D). In side-view the protoplasts were pear-shaped, the protoplasmic connections starting from very near their base. The connections were thin, but not very delicate, and were disintegrating except in a few places. The protoplasts measured 5–7 μ in diameter when young, but the older ones appeared slightly smaller, being 4–6·5 μ in diameter. Even in very old colonies the protoplasts were very close together, the distance between the lateral surfaces of the adjacent protoplasts being 1·5 μ at the posterior end and 2–3 μ at the anterior end of the colony.

Asexual colonies.—The only asexual colonies found contained well-developed daughter-coenobia (generally four to six), which were large and so closely packed inside the parent that they were closely invested by the latter, which presented a distended lobed appearance (text-fig. 7, I). These daughter-coenobia measured 220–250 μ in diameter.

Sexual colonies.—All the sexual colonies observed were female, and no evidence was obtained of the presence of any antheridia in these colonies, but in view of the poor condition of the material this could not be established with absolute certainty. If, as seems probable, there were separate male colonies, they must have disintegrated some time previously, after the escape

of the spermatozoids. It is probable therefore that the alga was dioecious. The number of oospores in the colonies was 50–128 (50, 64, 75, 78, 128 in different colonies). The ripe oospores were clothed with strong conical spines,

TEXT-FIG. 8.
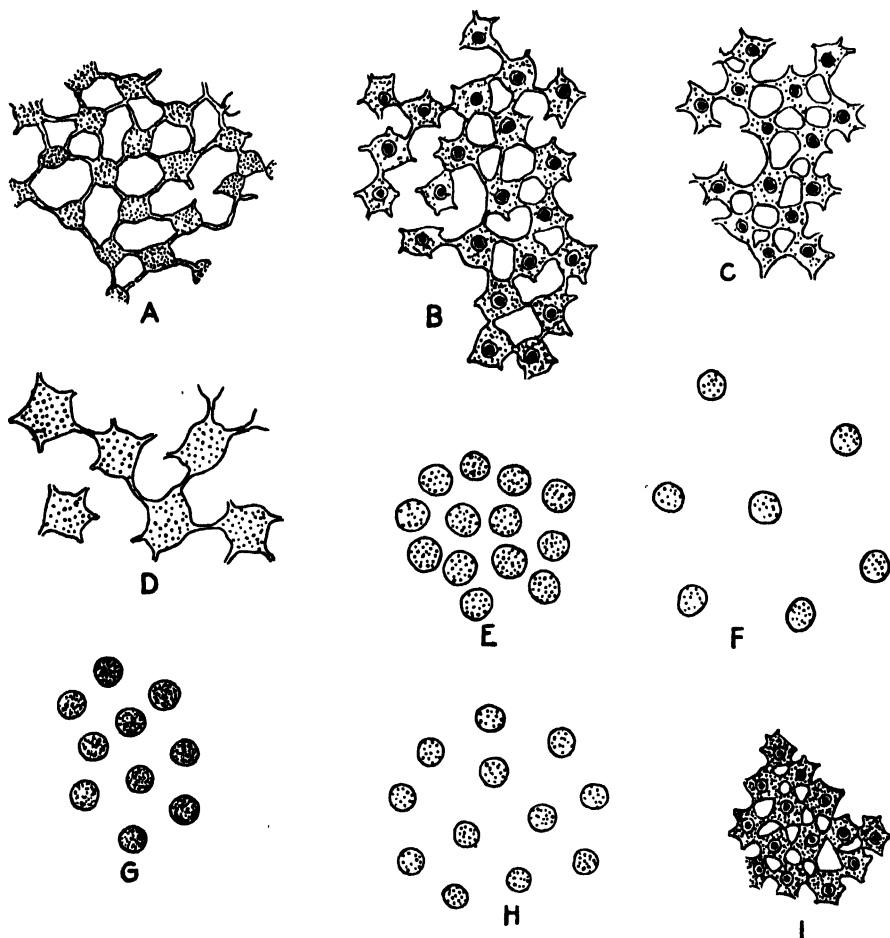
Surface-view of the protoplasts of diverse species of *Volvox*.

A, *V. prolificus*, sp. n.; B, *V. Rousseleti* West var. *lucknowensis*, nov.; C, *V. globator* Ehrenberg var. *maderaspatensis*, nov.; D, *V. Merrilli* Shaw f. (?); E, *V. dissipatrix* (Shaw), comb. nov.; F, *V. Carteri* Stein f. *nagariensis*, nov.; G, *V. africanus* West f. *minor*, nov.; H, *V. Carteri* Stein; I, *V. globator* Ehrenberg. (A–C, E–I, × 590; D, × 1115.)

broad below and tapering to a sharp point above, often slightly curved at the tip (text-fig. 9, F). The length of the spines was 9·5–10·5 μ. The spores without the spines measured 34–39 μ in diameter, fourteen to sixteen spines

being visible at the periphery in optical section. The oospores were distributed over most of the colony, except for a very small area (about one-sixth or less of the whole colony) near the anterior end.

In the form of the protoplasts, in the character of the oospores, in the number of oogonia, and to some extent in the size of the coenobia, this form comes very close to *V. Merrilli* Shaw. The great distention of the asexual coenobia by the daughter-individuals giving them a lobed appearance is very characteristic. The mature asexual coenobium of *V. Merrilli* with the daughter-individuals fully developed was, however, not present in Shaw's material, the largest daughter-coenobia found by him being 80 μ in diameter (Shaw, 1922, p. 495). Since some uncertainty also remains as regards the monoecious or dioecious character of my material, it is not easy to say whether the form here described is identical with *V. Merrilli*.

VOLVOX GLOBATOR (L.) Ehrenberg. (Text-fig. 8, I ; text-fig. 9, B.)

This species was collected by Dr. M. A. Sampathkumaran in a pool near Bangalore, occurring in such large numbers as to give a greenish colour to the water. The globose to subglobose coenobia measured 264–408 μ in diameter and contained 2,000 to 8,000 cells. The somatic protoplasts were star-shaped and measured 4–7 μ in diameter, the protoplasmic connections being fairly thick and appearing as prolongations of the angles of the protoplasts (text-fig. 8, I). The cell-walls formed a pentagonal or hexagonal pattern in surface-view, and appeared rectangular in side-view. In the asexual colonies up to seven daughter-coenobia were formed.

The sexual colonies contained oogonia only, but in each a few (up to five) spaces could be found, evidently representing the positions of former antheridia from which the spermatozoids had escaped. The colonies were therefore monoecious and protandrous. The number of oogonia was eighteen to thirty-five. The ripe oospores had a smooth inner and a spinous outer membrane, the short and conical spines having a broad base (text-fig. 9, B). The spores measured 35–44 μ without the spines, which were 3·5–7 μ long, the average length being about 5 μ ; fourteen to sixteen spines could be counted around the periphery in optical section.

VOLVOX DISSIPATRIX (Shaw), comb. nov. (*Copelandosphaera dissipatrix* Shaw *). (Text-fig. 5, H–K ; text-fig. 7, C ; text-fig. 8, E ; text-fig. 9, H.)

This alga was collected by Dr. M. A. Sampathkumaran from a greenish pool near Bangalore. There were present subglobose asexual and monoecious sexual colonies ; the latter were ellipsoidal when young, though later sub-globose, slightly longer than broad and somewhat narrower at the posterior end. The asexual coenobia reached 935 μ (697×748 μ, 842×867 μ, 867×935 μ) and the sexual ones 1037 μ (646×697 μ, 842×884 μ, 952×1037 μ) in diameter. On one occasion two sexual colonies, which were 1495 μ and 1815 μ in diameter

* Shaw, 1922 a,

respectively, were found, but very old colonies often measured nearly 2 mm. in diameter. The number of cells in the sexual coenobia was 12,000 to 20,000, and in the asexual ones 14,000 to 26,000.

The protoplasts are round in surface-view (text-fig. 5, K, I ; text-fig. 8, E) and elliptic-ovate or broadly pear-shaped (with the broader end directed outwards) in side-view (text-fig. 5, H, J) ; they are 6 μ wide and 7·5 μ high. The distance between the centres of adjacent protoplasts varies between 8 and 22 μ, as one passes from the posterior to the anterior end of the colony. The cell-wall consists of a delicate but comparatively firm layer immediately next to the protoplast (text-fig. 5, H) and a broad gelatinous outer layer with a definite boundary. The outlines of the cell-walls are generally pentagonal or hexagonal in surface-view (text-fig. 5, K) and rectangular in side-view. A single pyrenoid can be seen in each protoplast towards the posterior end (text-fig. 5, J). Under high magnifications a very slight bulging of the gelatinous envelope is recognisable on the outside of each protoplast (text-fig. 5, H). The protoplasts at first sight appear to have no protoplasmic connections, but under very high magnifications, after staining with aqueous methylene-blue or toluidine-blue or alcoholic safranin, extremely fine and delicate connections are recognisable between the cells. They are much finer than the cilia. Adjacent protoplasts are generally connected by two such strands (sometimes three), which often meet at a slight angle when they reach the boundary of the wall (text-fig. 5, I–K).

Asexual colonies.—From three to ten daughter-coenobia are formed inside the mother-colony, the usual number being 4–6 (text-fig. 7, C). The shape of the daughter-coenobia varies between ellipsoid and globose, and before liberation they measure 221–323 × 247–382 μ. Each escapes from the parent colony through a separate circular to elliptical hole, as Shaw (1922 a, p. 217) noticed in his Philippine material. The gonidia of the daughter-coenobia differentiate at a rather late stage, but before the new colony escapes from the parent.

Sexual colonies.—The front fourth of the colony is free from sexual reproductive bodies. Only a few antheridia (up to six) are formed in the sexual coenobia, and these are found nearer the anterior end. The antheridia form round sperm-platelets, which measure 37–40 μ in diameter and 10–11 μ in depth. The number of spermatozoids appears to be about 256. The number of oogonia is about seventy to ninety and the oospores have a smooth double wall (text-fig. 9, H) and measure 37–40 μ in diameter.

The alga just described agrees in most respects with *Copelandosphaera dissipatrix* Shaw. The dimensions of the asexual coenobia and the number of daughter-coenobia formed, however, appear to be somewhat smaller than in the Philippine material. Shaw describes this species as lacking protoplasmic connections between the cells. Through the kindness of Prof. Fritsch I was able to examine some of the material of *Copelandosphaera dissipatrix* distributed by Shaw, and found that, after staining in the way described on

Text-fig. 9.
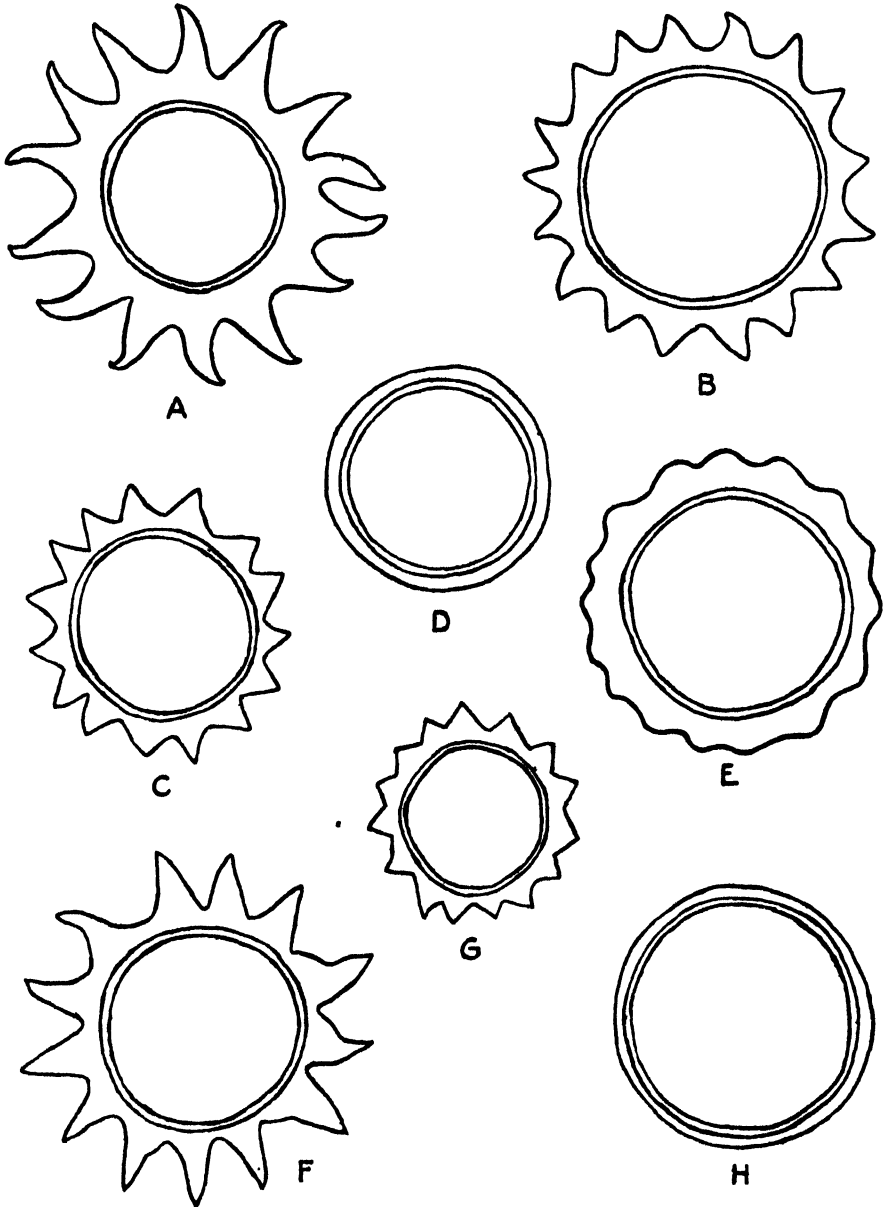
Oospores of diverse species of *Volvox*.

A, *V. globator* Ehrenberg var. *maderaspatensis*, nov.; ·B, *V. globator* Ehrenberg;
C, *V. prolificus*, sp. n.; D, *V. africanus* West f. *minor*, nov.; E, *V. Carteri* Stein;
F, *V. Merrilli* Shaw f. (?); G, *V. Rousseleti* West var. *lucknowensis*, nov.; H, *V. dissipatrix* (Shaw), comb. nov.   (All × 785.)

p. 357, delicate protoplasmic strands were recognisable under high magnifications ($\times$2,000 to 3,000), also in his material. These connections, however, are easily missed.

After discovering them in this species, I was led to apply the same methods to other forms in which the cells are believed to be devoid of protoplasmic connections. I examined in this way the following species :—*V. africanus* (Shaw's Philippine material and my own, cf. below), *V. Carteri* (own material, cf. p. 362), *V. Carteri* var. *manillana* (Shaw's material), *V. Carteri* f. *nagariensis* (own material, cf. p. 364), and a *Volvox* collected by Mr. D. J. Scourfield, I.S.O., from Epping Forest and showing much resemblance to *V. mononae* G. M. Smith (1920, p. 99, pl. 18, fig. 1). In none of these forms could protoplasmic connections be detected, although in each coenobia of very different ages (from very young to very old) were examined.

Meyer (1896, p. 200, pl. 8, fig. *a*) states that he found delicate protoplasmic connections in the unborn daughter-colonies of *V. tertius*, although he could not find them in the older colonies. The presence of connections in the young coenobia of *V. tertius* may constitute a recapitulation of a phylogenetic feature. In that case we should have to regard the species of *Volvox*, devoid of protoplasmic connections, as the more specialised and as derived from those possessing such connections.

The discovery of protoplasmic connections in *Copelandosphaera dissipatrix* brings this species nearer Shaw's *Janetosphaera*. It would be interesting to know whether the second species (*V. spermatosphaera* Powers), which Shaw includes under *Copelandosphaera* as *C. spermatosphaera* (Powers) Shaw, also possesses these protoplasmic connections.

VOLVOX AFRICANUS West f. MINOR, nov. (Text-fig. 6, I–K ; text-fig. 7, B, D, H ; text-fig. 8, G ; text-fig. 9, D ; Pl. **28**. figs. 14, 21, 22.)

This alga was collected by Dr. M. A. Sampathkumaran in a small pool on the top of the Nandhi Hill, near Bangalore, in the Mysore Province.

The colonies were asexual or sexual, the latter being unisexual or hermaphrodite. The asexual colonies were ovoid to ellipsoidal, the posterior end being broadly rounded and somewhat distended by the contained daughter-colonies, while the anterior end which was free from daughter-colonies was much narrower (text-fig. 7, H ; Pl. **28**. fig. 21). The sexual colonies were ellipsoidal, the female with a slightly broader anterior end (Pl. **28**. figs, 14, 22). All the three kinds of colonies are slightly flattened along an antero-posterior plane. When mounted in water on a slide, they rest on one of their flattened surfaces, so that only their broader surfaces are seen, but when crowded some of them rest on their narrower surfaces and the flattening of the coenobium is manifest. Occasional colonies are strongly flattened, but the majority are only slightly compressed ; the shape of a cross-section at right angles to the plane of flattening would probably be broadly oblong-elliptic (text-fig. 7, B, D).

2 D 2

The asexual coenobia measured 187×238–$289 \times 416\ \mu$, the female and bi-sexual 170×204–$331 \times 374\ \mu$, and the male 190×231–$248 \times 306\ \mu$. The number of cells in the colony varied from 1,400 to 3,000.

The protoplasts are round in surface-view (text-fig. 6, J ; text-fig. 8, G) and pear-shaped or ovoid (with the broader end directed outwards) in side-view (text-fig. 6, I, K, L). They measure 5–6·5 μ in diameter. They are more closely placed at the posterior than at the anterior end of the colony, the distance in one colony between the edges of the protoplasts being 9 μ at the anterior and 2–3·5 μ at the posterior end. There are no protoplasmic connections between the cells. The cell-walls are well seen when stained with aqueous methylene- or toluidine-blue or with alcoholic safranin. The last-named stain, although it tends to distort the shape of the colony, brings out the details fairly clearly. In surface-view the outermost part of the cell-walls forms a pentagonal or hexagonal network, within each compartment of which a second elliptic membrane is discernible separated by a wide space from the central rounded protoplast (text-fig. 6, J). Immediately adjacent to the protoplast is found a delicate membrane representing the innermost layer of the gelatinous wall. The same features are seen in the side-view, where the outline of the cell as a whole appears rectangular (text-fig. 6, I, K). The exact morphological significance of the second elliptic layer of the envelope is not clear.

In older colonies the outline of the outermost common envelope, as seen in optical section under higher magnifications, presents a slightly wavy appearance owing to its being slightly bulged out opposite each cell (text-fig. 6, L). This feature was more prominent at the anterior than at the posterior end.

Asexual colonies.—The asexual colonies usually form two daughter-coenobia (text-fig. 7, D, H ; Pl. 28. fig. 21), although one, three, or four are frequently found. When two are produced, they are arranged opposite each other in the middle region of the parent colony. The fully developed daughter-coenobia finally come to lie near the broad posterior end of the latter, so that the posterior poles of the two elongate daughter-individuals are very close to the posterior end of the mother-colony (text-fig. 7, H ; Pl. 28. fig. 21). When three daughter-individuals are formed, the third is placed behind and between the two median coenobia, a little towards the posterior end. When there are four coenobia, two are located in the middle opposite each other, and the remaining two behind these and alternating with the first pair. The median pair of coenobia are always the largest, when more than two are present. The young coenobia are slightly compressed and ovoid in form, with their long axis parallel to the longitudinal axis of the parent coenobium. A thin gelatinous vesicle, the remains of the gelatinous wall of the gonidium, is seen round each daughter-coenobium.

Sexual colonies.—The sexual colonies were not as numerous as the asexual ones, and the male colonies were very rare. The latter contain 50–180 antheridia which occur over nearly the whole of the male colony, only about the anterior eighth (or even less) being free from antheridia (Pl. 28. fig. 22).

The antheridia are thus very crowded and it is difficult to count their exact number. They measure up to 20 μ in diameter, while the platelets of spermatozoids measure up to 22 μ in diameter and 22 $\times$ 13 μ in side-view. There were 128 spermatozoids in each antheridium. No free spermatozoids were observed, though the cilia were fully formed on the cells in the platelets. The spermatozoids in the bundle measured 8–10 μ long and about 1·5 μ broad.

Some colonies were purely female, but most of them were bisexual containing from one to three, sometimes four, antheridia in the middle region of the coenobium. The number of oogonia in the female colonies varied between six and twenty-two (though in one colony as many as fifty-five oogonia were found), the bisexual colonies generally containing more oogonia than the purely female ones. The ripe oospores have a smooth wall of two layers and measure 30–39 μ in diameter.

As the above account shows, the Indian form agrees very closely with *Volvox africanus* as originally described by West (1910, 1918), and as subsequently amplified by Shaw (1923) from Philippine material. Neither West nor Shaw noted the slightly flattened nature of the coenobia. I have been able to examine one of West's slides made from the original material of *V. africanus* *, and also the material distributed by Shaw under the name of *Merillosphaera africana*. In both the slight flattening was observable, though not to the same extent as in the Indian alga.

West, in his first paper (1910), stated that there were no protoplasmic connections, but in the second paper (1918, p. 426) the occurrence of such connections is mentioned in the tabular statement; this was probably an error. Shaw found no protoplasmic connections in his material, nor does the Indian alga show any (cf. also p. 359).

West pointed out that the gonidia in the daughter-coenobia were well differentiated long before birth and, as noted by Shaw, they attain considerable size before they divide. Both West and Shaw observed a few colonies of the third generation with gonidia already differentiated, so that four generations were represented in one individual. In my material colonies showing three generations are extremely common, and there are occasional ones in which four generations are represented.

Though the Indian alga shows very close agreement in all essential respects with the African and Philippine material, there are some minor differences. The colonies of the Indian alga are much smaller than those previously described, measuring only 238–408 $\times$ 187–289 μ, whereas the African one measured 345–610 $\times$ 295–480 μ and the Philippine form 345–600 $\times$ 295–500 μ. The asexual colonies in the African and Philippine material are somewhat narrowed instead of being broadly rounded posteriorly, and the daughter-coenobia are not so close to the posterior end, as in the Indian alga. While the number of gonidia and daughter-coenobia formed in the Indian alga is generally two, West's photographs show three to four, and in the above-mentioned slide

* By the courtesy of Prof. W. Stiles, F.R.S.

four to six are present. Shaw records one to eight daughter-coenobia. The Indian alga also differs in the small number of oogonia and in the smaller size of the oospores, although Shaw records a smaller number of oogonia (12–32) than West found in the African material (70–80).

The small form, occasionally found by Shaw (1923, pp. 205–208, pl. 6, figs. 43–45) in a pure condition, is probably identical with the Indian alga, with which Shaw's description and photographs agree in many ways. Thus, he describes the coenobia as sometimes broader than long, and measuring 150–270 × 160–240 μ ; asexual coenobia having usually two daughter-coenobia ; oogonia fifteen to twenty-seven in number ; and the oospores 35–43 μ in diameter. Unfortunately, the specimens he photographed were very much contracted in the venetian turpentine mount, so that one cannot get a good idea of the shape of the colonies from the photographs. The posterior end of the colony in the photograph, however, appears to be broadened somewhat as in the Indian alga. I consider this alga a new form of *V. africanus* West, which may be named f. *minor*.

VOLVOX CARTERI Stein.* (Text-fig. 6, D, E, F ; text-fig. 7, E ; text-fig. 8, H ; text-fig. 9, E ; Pl. 28. figs, 16, 19, 25.)

This alga was collected by Mr. M. O. T. Iyengar in January 1916 in some small pools, on the point of drying up, in the bed of a tank in Mylapore, Madras.

The coenobia are asexual, male or female. The asexual coenobia are globose to subglobose, and measure 460–630 × 485–646 μ (460 × 485 μ, 560 × 578 μ, 578 × 612 μ, 630 × 646 μ). The female coenobia are subglobose, and measure up to 578 × 612 μ. The male coenobia are very small, ellipsoid to globose, and attain only to 221 × 238 μ. The asexual colonies have 3,000 to 11,000 cells, the female 2,000 to 3,000, and the male 500 to 700.

The protoplasts are round in surface-view and are 4·5–5·5 μ wide and 5·5–6·5 μ high (text-fig. 6, E ; text-fig. 8, H). The distance between the edges of the adjacent protoplasts is 3·5–5·5 μ at the posterior and 8·5 μ at the anterior end of the colony. No protoplasmic connections could be detected, although the same methods to render them visible were used as were successful in *V. dissipatrix*. The outlines of the actual cells are pentagonal or hexagonal in surface-view (text-fig. 6, E) and somewhat rectangular in side-view (text-fig. 6, D). The actual depth of the cells is 14–16 μ from outer to inner wall. The cell-wall consists of a firm though delicate inner layer, immediately surrounding the protoplast, and of a broad gelatinous outer portion. In the preserved material the protoplasts have contracted somewhat, and the inner layer of the wall can be seen as a delicate ring round each protoplast.

Asexual coenobia.—From three to eight daughter-colonies are found in the asexual coenobia, but the usual number is four to six. Generally four gonidia,

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* *Volvox globater* Carter non Ehrenberg (Carter, 1859, pp. 2–5, 18, 19, pl. i. figs. 1, 3, 4, 7, 8, & 10); *Volvox Carteri* Stein (1859–83, Abth. iii. p. 134); *Merillosphaera Carteri* (Stein) Shaw var. *typica* Shaw (Shaw, 1922, xxi, p. 87 et seq.).

dividing to form daughter-coenobia, are arranged more or less equidistantly in the middle region of the parent colony, while the remainder are situated towards the posterior end and alternate with the others (text-fig. 7, E ; Pl. **28.** fig. 16). The middle four are usually larger than the others, which appear to be younger, and are often merely represented by undivided gonidia, at a time when the middle ones are well-developed daughter-coenobia, whose gonidia are already differentiated. The daughter-coenobia inside the parent measure 165–238 μ in diameter. The young individuals found in the asexual coenobia in my material were all either male or asexual or partly asexual and partly male. None were female.

Female coenobia.—These were very scantily represented as compared with the asexual coenobia. From 17 to 29 oogonia were observed (Pl. **28.** fig. 19). The oospores had a smooth inner wall and a wavy crenate outer wall (text-fig. 9, E ; Pl. **28.** fig. 25). The spores measure 42–47 μ in diameter.

Male coenobia.—There were young male coenobia inside the asexual colonies, but only a few were found free. The antheridia begin to divide in the daughter-coenobia, while they are still inside the mother. There were about seventy-five and these occupied almost the whole of the colony, except at the extreme anterior end. The undivided antheridial cells are about 14 μ wide. The antheridial cells, in the few free male colonies observed, were dividing into two or four cells, but fully formed antheridia were not seen in the material.

The alga just described resembles very closely the one collected by Carter (1859) in Bombay, and described by him under the name of *V. globator.* Stein (1859–83) later established Carter's form as a new species, *V. Carteri*, basing his diagnosis on Carter's account of the Bombay *Volvox.*

The dimensions of Carter's alga are given in fractions of inches, but reckoned in micromillimetres they are as follows :—The adult spherical or nearly spherical asexual coenobium measures 770 μ, the female coenobium 608 μ, the male 270 μ, and the young daughter-coenobia about 192 μ. The daughter-colonies are stated to be very regularly arranged and generally to be eight in number. They contain, while still inside the parent, well-differentiated gonidia, reaching up to 85 μ before division. The cells are described as globular, and Carter's figures show that they were devoid of protoplasmic connections, and that the innermost layer of the cell-wall had a structure somewhat similar to that above described for my specimens. Carter found either male or female daughter-coenobia along with asexual ones in the same individual, but did not find the male and female coenobia in the same parent. He also points out that one, several, or all the daughter-individuals of a colony may be male. The female coenobia contained thirty to fifty oogonia, the oospores being 40 μ in diameter, and having a slightly wavy outline.

This description agrees so closely with that of the Madras *Volvox* that the two are no doubt identical. The female daughter-coenobia within the parent-colony are described by Carter as attaining double the size of a male daughter-coenobium, but my material did not enable me to check this point.

Since Carter described this *Volvox*, it has only been once recorded. Playfair (1918, p. 527, pl. 56, figs. 21, 22) records it from the Lismore District. He describes the oospores as wavy when young, but spiny when fully developed. He has a drawing of the spiny oospore, but does not give any figures or photographs of the colonies, nor does he give any proper description of them. The oospores examined by me were fully ripe, with both walls well developed, and the membrane was invariably crenate. Shaw found the same in the Philippine material referred to a variety (cf. below). In the absence of a proper description and figures or photographs of the colonies, it is not possible to be sure that Playfair's *Volvox* was really *V. Carteri*. It must be pointed out that he did not see Carter's paper, but identified his *Volvox* from the casual reference to the crenate oospores of *V. Carteri* by Lemmermann (1904, p. 105). The oospores in all species of *Volvox* having spiny oospores have wavy walls when young and develop the spines when they become older.

VOLVOX CARTERI Stein forma NAGARIENSIS, nov. (Text-fig. 7, A ; text-fig. 8, F ; Pl. 28. fig. 18.)

Occasional colonies of this alga were found among those of *V. prolificus* in the pool in the bed of the river Nagari. Only globose asexual coenobia were present, but these were sufficiently characteristic to warrant a reference to *V. Carteri*. They measured up to 1003 μ in diameter and comprised up to 8,000 cells.

The protoplasts were round in surface-view (text-fig. 8, F) and pear-shaped in side-view. They measured 6–7 μ in diameter and up to 9 μ in length. The cell-wall shows the structure described on p. 362. The distance between the centres of adjacent cells in an old colony was up to 30 μ. There were no protoplasmic connections. The number of daughter-coenobia was large, sometimes as many as twenty-one, the usual number being about fifteen (text-fig. 7, A ; Pl. 28. fig. 18). Their arrangement could not be easily recognised. The daughter-coenobia were slightly ellipsoidal and measured from $123 \times 138 \mu$ to $340 \times 357 \mu$ before liberation. The daughter-coenobia were all asexual and contained well-developed gonidia, those in one daughter-coenobium about to escape measuring 26–30 μ in diameter at a time when the somatic protoplasts were only 4–5 μ in diameter.

This form differs from *V. Carteri* Stein and from *V. Carteri* Stein forma *mánilana* (*Merillosphaera Carteri* (Stein) Shaw var. *manilana* Shaw*), and *V. Carteri* Stein forma *Weismanniana* comb. nov. (*V. Weismannia* Powers † ; *Merillosphaera Carteri* (Stein) Shaw var. *Weismannia* (Powers) Shaw ‡) in the larger dimensions of the asexual coenobia and in the larger number of daughter-

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* Shaw, 1922 *b*, pp. 90–104, 120–1.

† Powers, 1908, pp. 152–162, 172–5.

‡ Shaw, 1922 *b*, pp. 107–110, 121.

colonies produced. It appears to be no more than a form of *V. Carteri* Stein, which may be named f. *nagariensis*.

THE CLASSIFICATION OF THE SPECIES OF VOLVOX

The cell-structure in all species of *Volvox* shows a considerable degree of uniformity. The cells have thick gelatinous walls, the outlines of which as a result of mutual pressure form a polygonal network in surface-view. The second membrane, between the external and internal boundaries of the wall, above recorded for certain species of *Volvox* without protoplasmic connections, is at present difficult to explain, nor is it clear how far it is represented in other species. The relatively small protoplasts, though varying somewhat in shape, appear to show a rather uniform structure. The main difference in cell-structure among the species lies in the presence or absence of protoplasmic connections.

Shaw has classified the existing species of *Volvox* into two groups, according as protoplasmic connections are present or absent between the cells. The species lacking protoplasmic connections he has placed under four genera, mainly based on the stage at which the gonidia differentiate in the embryos. Such differences, while they appear constant for a given species, scarcely seem sufficient to warrant the establishment of separate genera, in view of the general similarity in cell-structure. Moreover, *Copelandosphaera* has been shown above to possess protoplasmic connections (cf. p. 359), while the character (viz. the migration of the gonidia from without into the interior in the young embryo) on which *Campbellosphaera* (Shaw, 1919) was mainly based, is due to the inversion of the embryo, a phenomenon which is now known to occur in all colonial members of Volvocales.

The fundamental features, apart from cell-structure, on which the species of *Volvox* can be distinguished are the distribution of the sexes, the numbers of the reproductive cells, and to some extent the disposition of the gonidia, especially when there are few of these. *V. prolificus* is essentially distinguished by the consecutive formation of all three kinds of reproductive cells and by their large numbers.

A further feature that is apparently of systematic importance is the character of the oospore, although further experience is wanted to assess the value of the relatively slight differences between the spines on the spores of diverse species.

It may be emphasised that the description of the forms of *Volvox* dealt with above is based mostly on the investigation of a considerable bulk of material and that this has displayed a considerable constancy in certain features —even, sometimes, in minor particulars. Until extensive culture-experiments have been carried out, however, it is scarcely possible to say how far some of them may represent local habitat-forms. In any case their careful description has, I hope, added to our knowledge of the forms of *Volvox* as they occur in nature.

ORGANISMS OBSERVED ON PANDORINA,
EUDORINA, AND VOLVOX

(1) A unicellular epiphyte resembling *Craniocystis bipes* Korschikoff (Printz, 1927) was often seen on the colonies of *Pandorina morum, Eudorina elegans,* and *E. illinoisensis* (text-fig. 10, E, G), without apparently doing any harm to them. Usually only one or two individuals were found on a colony, and these were restricted to the posterior portion. The shape of the chloroplast of the epiphyte could not be clearly made out, but it contained two or three pyrenoids. The cells were enveloped by two membranes, the inner fairly firm, and the outer very thin and delicate. The outer wall bore at its base two very small, slightly toothed processes, by means of which the epiphyte was attached to the outer gelatinous sheath of the colonies (text-fig. 10, G). In the type-species the attaching processes are not toothed, but appear to be disc-shaped. Empty envelopes with the apex ruptured (text-fig. 10, E) were often found, suggesting reproduction by motile spores. The full-grown cells measured about 18 μ high and 20 μ broad.

(2) In another unicellular epiphyte (text-fig. 10, A, F), found on the colonies of *Volvox prolificus*, the cell was rounded in surface-view, while in side-view it was broadly ovate, with the apical portion beaked, as in text-fig. 10, A. The chloroplast appeared to be bell-shaped, with the opening directed towards the point of attachment. Two to four pyrenoids were present in the chloroplast. In a few cells the protoplast had divided into 8, 16, or 32 parts. The cells measured 16–18 μ in diameter and were 14–16 μ high.

(3) A Chytridiaceous parasite (text-fig. 10, B–D, I) was commonly observed on the colonies of *Pandorina morum, Eudorina elegans,* and *E. illinoisensis*. The external part of the parasite was somewhat globose with a rounded apex, and from it a thin haustorial process extended into a cell of the host, gradually absorbing the contents, while the part outside the host became bigger. The lower end of the haustorium, in contact with the host-cell, also becomes slightly swollen (text-fig. 10, B). The protoplast of the cell attacked gradually shrivels, and finally only a minute residue is left. The parasite may attack several cells of a colony successively, and it is not uncommon to find colonies with one or more cells missing through its activities (text-fig. 10, B–D). The empty ruptured envelope of the parasite is often found attached to such colonies. The rupture is broad and apical (text-fig. 10, B, D). It seems probable that the contents of the fungal cell escape as motile spores, which in their turn attack other colonies, but the actual escape of spores has not been observed. The fully developed fungal cell was 16 μ broad and 14 μ high, the haustorial process being about 9 μ long.

This parasite closely resembles *Rhizidium Pandorinae* (Wille) Fischer (Fischer, 1892, i, Abt. iv. 1892, p. 109=*Chytridium Pandorinae* Wille, 1884, p. 46), which Wille has recorded as attacking *Pandorina morum* in South America. The American fungus differs from the Indian one, however, in the fact that the apex of the cell is produced into a kind of beak, and that the zoospores escape

by a lateral orifice (text-fig. 10, H). The Indian form may be regarded as a new variety, var. *globosa* *, of Wille's form, differing in the broadly rounded apex and the spores escaping by a wide apical aperture.

(4) In the formalin material of *Eudorina elegans* the cells of certain colonies showed a peculiar appearance. The cilia were crumpled or shrivelled up close to the surface of the colony, looking like a singed hair. When stained with erythrosine, the cells showed a dense cobweb-like covering of somewhat dark matted threads which did not take up the stain. Often the cells were completely surrounded by this covering, but sometimes it occurred only on one side. At a later stage the cells appear to lose their rounded shape and become somewhat flattened on their inner side, the two lower edges being slightly bent outwards. When all the cells assume this shape, they appear to touch one another. This at first gives the impression of a *Eudorina* colony in which the cells have developed protoplasmic connections. The fluffy covering around the cells does not appear to consist of fungal hyphae, but rather to be of bacterial (?) nature. The cilia appear first to be attacked, changing into a loose, more or less crumpled mass in which numerous rod- and dot-like fragments are to be seen. The disease seems to progress through the cilia into the colony and then to spread around the cilia. I was not able to detect any other details of structure and my main object in referring to this case is to point out the deceptive resemblance of the diseased alga to one having protoplasmic connections.

(5) In preserved material of *Volvox globator* var. *maderaspatensis*, the oospores in some colonies were attacked by an amoeboid parasite (*Vampyrella* ?) (text-fig. 10, J–M, O, Q, R). When the colony is stained with alcoholic safranin the parasite is at first seen closely attached to one side of the spiny oospores, within the gelatinous outer envelope of the latter (text-fig. 10, J). One or two processes then pierce the spiny wall and penetrate into the contents (text-fig. 10, K). Since an inner wall was not observable in these oospores, the parasite evidently attacks them before its formation. Finally the whole parasite enters the oospore (text-fig. 10, M), engulfing and finally absorbing the contents (text-fig. 10, Q). After some time it again escapes from the envelope of the oospore (text-fig. 10, L, R ; Pl. 28. fig. 10).

(6) In certain old colonies of *Volvox prolificus*, the protoplast of one or more oospores showed peculiar features, evidently as a result of the attack of an amoeboid parasite, which was often seen attacking the young oospores. Such oospores fail to form walls, but undergo great enlargement while still enclosed in the wide mucus-wall, which has also increased in size. The contents are very dense. These enlarged cells had in one instance divided into four (text-fig. 10, S), and in several instances into eight (text-fig. 10, N) and more large irregularly rounded cells of unequal sizes, which are often loosely grouped as an irregular hollow sphere and present an unhealthy appearance (text-fig. 10, P).

* *Rhizidium Pandorinae* (Wille) Fischer var. *globosa* nov. A typo differt apice latissimo et poro terminale.

TEXT-FIG. 10.
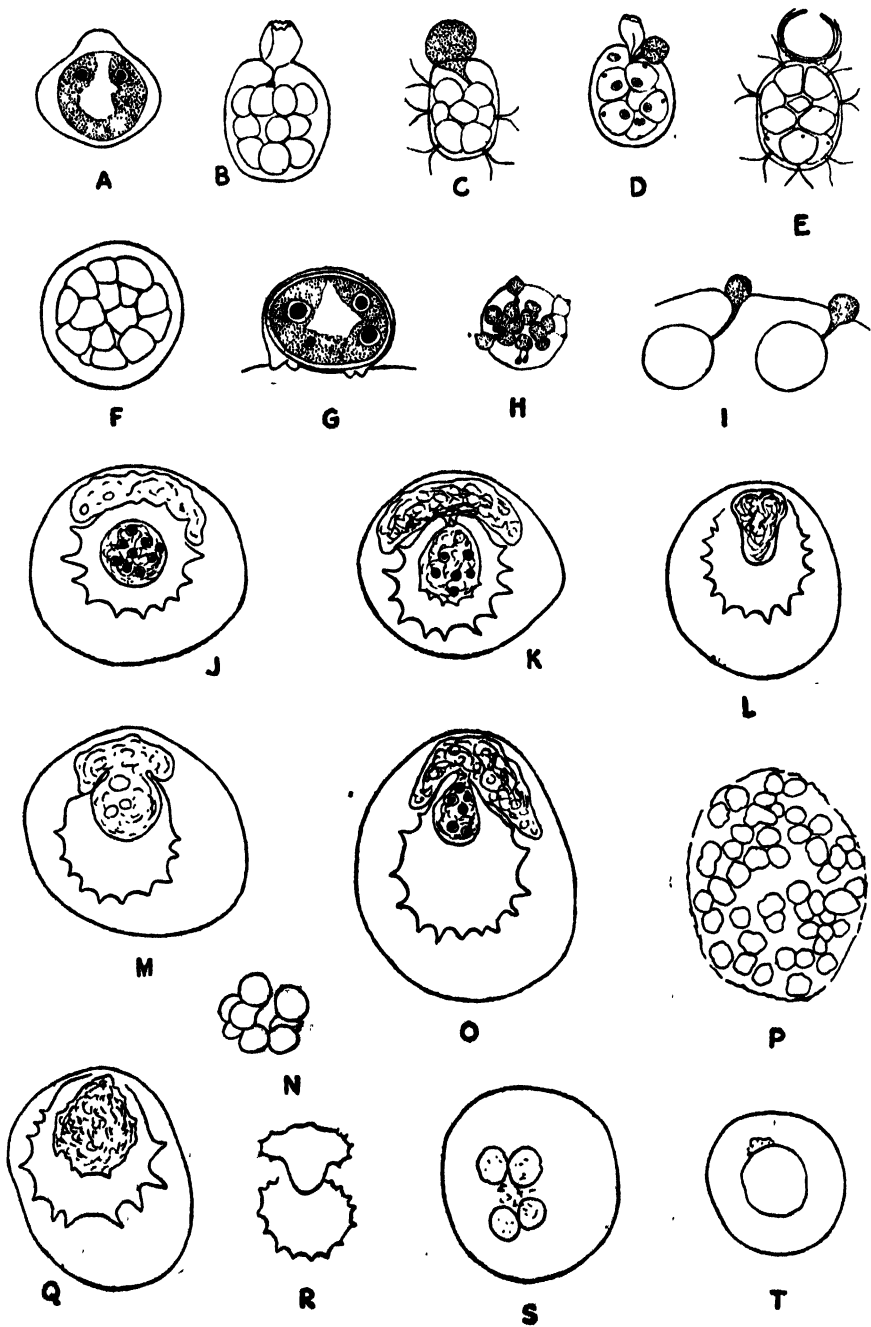
EXPLANATION OF TEXT-FIG. 10.

A, F, unicellular epiphytic alga on *V. prolificus*: A, from the side; F, from the surface, showing division of protoplast.

B–D, I. *Rhizidium Pandorinae* (Wille) Fischer var. *globosa*, nov.

C vegetation stage on *Pandorina morum*; B, empty cell of parasite after escape of contents; D, the two stages side by side; I, young individuals attacking cells of *Eudorina elegans*.

E, G. *Craniocystis bipes* Korschikoff f. (?); G, mature cell; E, empty cell.

H, *Rhizidium Pandorinae* (Wille) Fischer on *Pandorina morum* (after Wille).

J–M, O, Q, R, successive stages of an amoeboid parasite (*Vampyrella*?) attacking oospores of *Volvox globator* Ehrenberg var. *maderaspatensis* (see text p. 367).

N, P, S, T. oospores of *Volvox prolificus* dividing within the mother-colony, a pathological condition, probably due to the attack of an amoeboid parasite: T, the parasite in contact with the oospore; S, N, P, division of the protoplast of the oospore into 4, 8, and numerous parts respectively. Pyrenoids black.

(A, F, G, × 1200; B–E, × 400; H, × 190; I, × 745; J–T, × 390.)

(7) Rotifers are often seen infesting colonies of *Eudorina elegans*, *E. illinoisensis*, and those of species of *Volvox*. One species commonly attacked the colonies of *Volvox prolificus*. Sometimes as many as six individuals were seen inside a colony, but usually there were only one or two. Even very young colonies, sometimes still inside the parent, were occupied by this rotifer. Many of the colonies were partly devoured by the rotifers.

(8) On one occasion a kind of blood-worm was seen devouring large numbers of colonies of *Eudorina illinoisensis* kept in a dish in the laboratory at Madras.

(9) A protozoan epiphyte, resembling a small shortly stalked species of *Vorticella*, was found in large numbers on the surface of *Volvox globator* var. *maderaspatensis*. Animal epiphytes have so far not been recorded on *Volvox*.

DIAGNOSES OF NEW SPECIES, VARIETIES, AND FORMS

PANDORINA MORUM Bory f. MAJOR, nov. (Text-fig. 1, N, O, P, U, V; Pl. 28. fig. 7.)

Familiis e 32 vel saepe e 16 cellulis constantibus, pyrenoidibus 3–4 in cellulis maturis, plus numerosis in cellulis vetustis. Fam. 32-cell., 55–64 μ lat., 63–74 μ long. (55×63 μ, 57×63 μ, 57×68 μ, 61×68 μ, 64×74 μ); cellulae pyriformes, 11–15 μ lat., 12–14·8 μ long.

Hab. In rain-water pools along with other motile algae, in Madras.

EUDORINA INDICA, sp. n. (Text-fig. 3; Pl. 28. figs. 2, 12, 13.)

Familiis ellipsoideis, e cellulis 64 constantibus, cellulis in seriebus transversis 7 cum 4, 8, 12, 12, 12, 12 et 4 cellulis dispositis; iis series anterioris multo minoribus quam iis series secundae et iis series secundae minoribus quam iis serium reliquarum; cellulis serium anteriorum 2 probabiliter somaticis, iis serium reliquarum propagativis; pyrenoidibus ad 4 in cellulis serium anteriorum, ad 16 in cellulis serium reliquarum.

Familia 140–175 μ long., 110–131 μ lat.; cellulis series anterioris 8·75–12 μ lat., ser. secund. 10–14 μ lat., ser. reliq. 14–23·5 μ lat.

Hab. Talguppa, Mysore Province, in a rain water pool (*M. A. Sampath-kumaran*) ; Madras, in a rain-water pool.

PLEODORINA SPHAERICA, sp. n.   (Text-fig. 4 ; Pl. 28. figs. 4, 5.)

Familiis fere sphaericis, a cellulis 128 irregulariter in parte peripherica massae gelatinosae dispositis ; cellulis somaticis numerosis, in tota familia inter gonidia sparsis ; pyrenoidibus 1–3 in cellulis somaticis, ad 8 in gonidiis ; propagatione asexuali et sexuali ignota.

Fam., 187–210 μ lat. ; cell. somat., 9–11 μ lat. ; gonid., 15–17 μ lat.

Hab. Among other algae in a pool on a hill-slope at Vandalur, near Madras.

VOLVOX PROLIFICUS, sp. n.   (Text-fig. 5, A–G ; text-fig. 7, J ; text-fig. 8, A ; text-fig. 9, C ; Pl. 28. figs. 3, 6, 9, 20, 23.)

Familiis dioicis, in parte anteriori leviter dilatatis, in parte posteriori angustatis, asexualibus et femineis subglobosis vel globosis, masculinis ellip-soideis aut subglobosis, cellulis 9,000–25,000 ; protoplastis irregulariter rotundatis, 5–6 μ lat., processibus cytioplasmaticis angustis, in cellulis seni-oribus tenuibus et elongatis. Cellulis propagativis continue et successive per vitam in familiis efformatis. Familiis filialibus 4–20, plerumque 6–12, leviter ellipsoideis, 153–230 μ lat. ante nationem, gonidiis in familiis filialibus vix ante nationem efformatis ; antheridiis olim efformatis, 25–55, rotundatis, discoideis, 38–40 μ lat., spermatozoideis 13–15 μ long. et 0·8–1 μ lat., ciliis post apicem insertis ; oogoniis 100–500 ; antheridiis paucis in familiis juvenali-bus asexualibus vel femineis. Oosporis membrana externa cum spinis conicis robustis, 5–7 μ longis et membrana interna laevi munitis. Fam. asex., 400–1010 μ ; fam. masc., 400–800 μ ; fam. fem., 400–1070 μ ; oosp. sine spin., 30–35 μ lat.

Hab. In a drying pool in the bed of the River Nagari, near Tirupati, in South India (*M. S. Raghava Chari*).

VOLVOX ROUSSELETI West var. LUCKNOWENSIS, nov.   (Text-fig. 6, G ; text-fig. 7, F ; text-fig. 8, B ; text-fig. 9, G ; Pl. 28. figs. 8, 11.)

Familiis dioicis, subglobosis vel ellipsoideis, cellulis 6,000–8,000 ; proto-plastis late stellatis, 5·5–7·5 μ lat., processibus cytioplasmaticis tenuibus. Familiis filialibus ad 7 ; oogoniis numerosis, 160 vel pluribus ; antheridiis 20–60, 38–42, 5 μ lat., spermatozoideis ca. 256. Oosporis cum spinis brevibus, late conicis, 3·7–5·5 μ longis, munitis vel saepe cum membrana undulata.

Fam., 510–629×544–765 μ ; oosp. sine spin. 32–33·5 μ lat., oosp. crenat. 34–35 μ.

Hab. Lucknow (*A. R. Roa*).

VOLVOX GLOBATOR (L.) Ehrenberg var. MADERASPATENSIS, nov.   (Text-fig. 6, A–C ; text-fig. 7, G ; text-fig. 8, C ; text-fig. 9, A ; Pl. 28. figs. 10, 15, 24.)

Familiis monoicis, asexualibus subglobosis, sexualibus ellipticis vel elliptico-ovatis, cellulis 6,000–11,000 ; protoplastis irregulariter rotundatis vel stellatis,

processibus cytioplasmaticis tenuibus longis. Familiis filialibus 2–4, plerumque 2, in lateribus oppositis posteriore dispositis ; antheridiis paucis, jusqua 8 ; oogoniis 13–38. Oosporis cum spinis conicis robustis acutis saepe leviter curvatis, 8–13 μ longis, vestitis.

Fam. asex. ad 693 μ lat., fam. sex. ad 640×759 μ ; oosp. sine spin. 35–42 μ lat.

Hab. In a pool inside a *Casuarina*-plantation near Elliot Beach, Madras (*T. Ekambaram*).

VOLVOX AFRICANUS West f. MINOR, nov.   (Text-fig. 6, I–K ; text-fig. 7, B, D, H ; text-fig. 8, G ; text-fig. 9, D ; Pl. **28**. figs. 14, 21, 22.)

Familiis dioicis vel monoicis, leviter deplanatis, asexualibus ovoideis vel ellipsoideis in parte posteriori late et in parte anteriori anguste rotundatis, sexualibus ellipsoideis, cellulis 1,400–3,000 ; protoplastis a superficie visis rotundatis, a latere visis pyriformibus in parte exteriori dilatatis, processus cytioplasmaticos absunt. Familiis filialibus 2–4, elongato-ovoideis, plerumque 2 solum, in media parte familiae cum polis prope partem posteriorem familiae maternae dispositis ; antheridiis numerosissimis, in tota familia praeter sextam partem anteriorem dispositis, spermatozoideis 128 ; familiis femineis saepe bisexualibus, cum antheridiis paucis (ad 4) in media parte ; oogoniis 6–22, interdum ad 59. Oosporis cum membrana laevi.

Fam. asex., 187×238–289×416 μ ; fam. masc., 190×231–248×306 μ ; fam. fem., 170×204- 331×374 μ ; lat. oospor., 30–39 μ.

Hab. In a small pool on the top of the Nandhi Hill, near Bangalore, in Mysore Province (*M. A. Sampathkumaran*).

VOLVOX CARTERI Stein f. NAGARIENSIS, nov.   (Text-fig. 7, A ; text-fig. 8, F ; Pl. **28**. fig. 18.)

Familiis asexualibus solum notatis, globosis, cellulis ad 8,000, typo similis, sed familiis filialibus numerosis, ad 21, plerumque 15 ; protoplastis 6–7 μ lat., ad 9 μ long., a superficie visis rotundatis, a latere visis pyriformibus in parte exteriori dilatatis, processus cytioplasmatices absunt. Familiis filialibus subellipsoideis, 123×138–136×153 μ, gonidiis bene efformatis.

Diam. fam., ad 1003 μ.

Hab. In a drying pool in the bed of the River Nagari near Tirupati, South India, occurring sparsely among *Volvox prolificus* (*M. S. Raghava Chari*).

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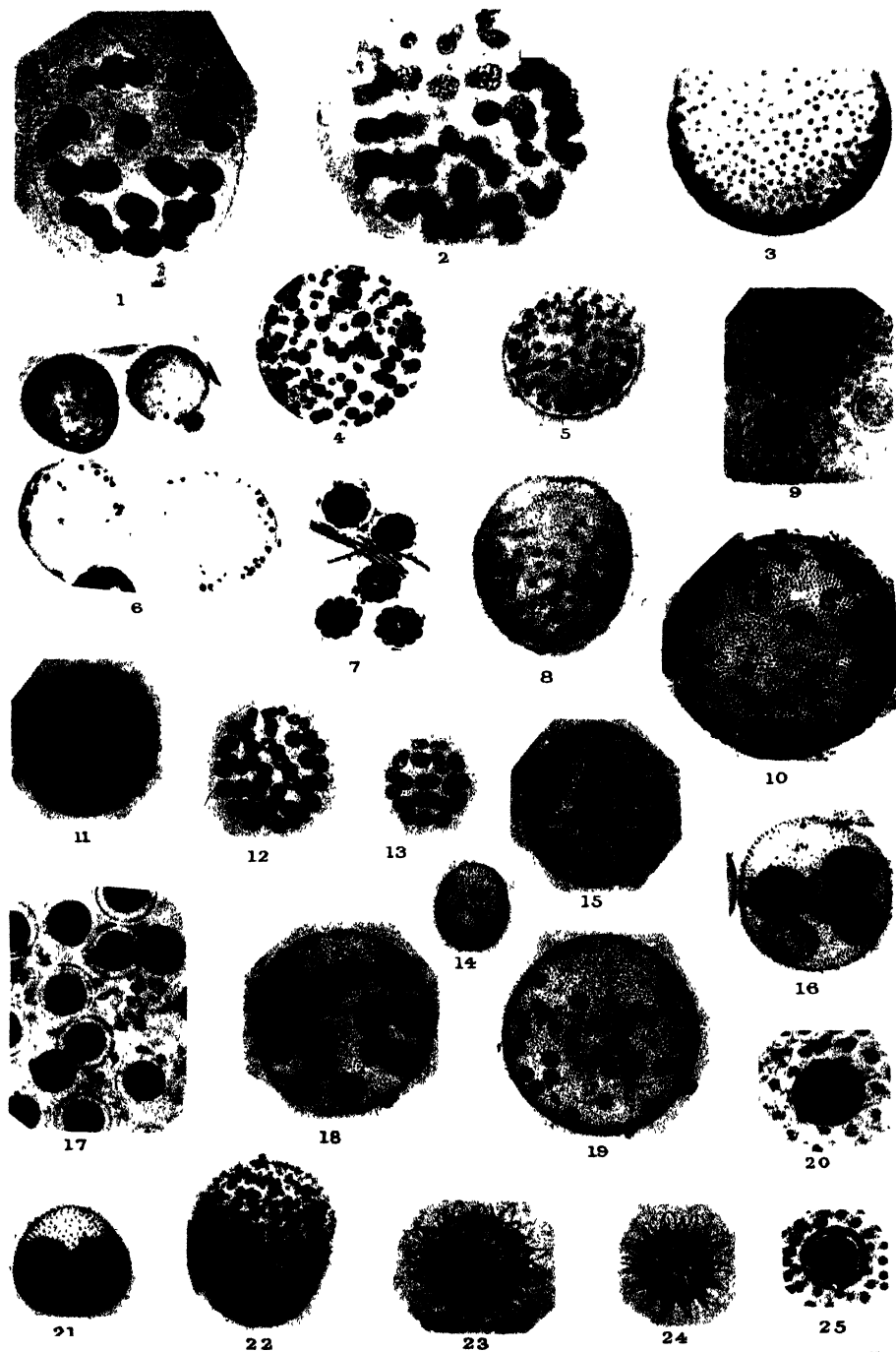
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EXPLANATION OF PLATE 28.

Fig. 1. *Eudorina illinoisensis* (Kofoid) Pascher, monoecious colony; the four front cells forming three antheridia and one 16-celled colony, the remaining cells forming oogonia. (× 240.)

Fig. 2. *Eudorina indica*, sp. n., cells dividing to form antheridia and daughter-colonies; the anterior cells are not dividing. (× 150.)

Fig. 3. *Volvox prolificus*, sp. n., female colony. (× 30.)

Fig. 4. *Pleodorina sphaerica*, sp. n., colony with mature gonidia. (× 115.)

Fig. 5. Colony of *Pleodorina sphaerica*, sp. n., with the gonidia beginning to enlarge. (× 35).

Fig. 6. *Volvox prolificus*, sp. n., showing diverse sizes of male colonies. (× 22.)

Fig. 7. *Pandorina morum* Bory f. *major*, nov. (× 100.)

Fig. 8. *Volvox Rousseleti* West var. *lucknowensis*, nov., female colony. (× 35.)

Fig. 9. *Volvox prolificus*, sp. n., showing polygonal outlines formed by the membranes of the oogonia. (× 165.)

Fig. 10. *Volvox globator* Ehrenberg var. *maderaspatensis*, nov., amoeboid parasites escaping from the oospores. (× 40.)

Fig. 11. *Volvox Rousseleti* West, var. *lucknowensis*, nov., male colony. (× 41.)

Figs. 12 & 13. *Eudorina indica*, sp. n., 64-celled and 32-celled colonies respectively (× 100.)

Fig. 14. *Volvox africanus* West f. *minor*, nov., female colony. (× 40.)

Fig. 15. *Volvox globator* Ehrenberg var. *maderaspatensis*, nov., colony with oospores. (× 30.)

Fig. 16. *Volvox Carteri* Stein, with three male and three asexual daughter-coenobia. (× 40.)

Fig. 17. *Eudorina elegans* Ehrenberg., spermatozoids around egg-cells. (× 520.)

Fig. 18. *Volvox Carteri* Stein f. *nagariensis*, nov. (× 30.)

Fig. 19. *Volvox Carteri* Stein., colony with oospores. (× 55.)

Fig. 20. *Volvox prolificus*, sp. n., antheridium. (× 265.)

Fig. 21. *Volvox africanus* West f. *minor*, nov., asexual colony with daughter-individuals. (× 45.)

Fig. 22. The same, male colony. (× 63.)

Fig. 23. *Volvox prolificus*, sp. n., oospore. (× 400.)

Fig. 24. *Volvox globator* Ehrenberg var. *maderaspatensis* nov., oospore. (× 240.)

Fig. 25. *Volvox Carteri* Stein, oospore. (× 210.)

A comparative study of Geotropism in three species of *Lupinus*.

By E. D. BRAIN. (Communicated by Dr. T. L. PRANKERD, F.L.S.)

(With 5 Text-figures)

[Read 19 January 1933]

INTRODUCTION

The species of *Lupinus* used for the experiments recorded below exhibit differences of growth and life-habit which make a comparative study of their geotropic behaviour throughout their life-cycle a very fascinating piece of work.

Lupinus albus is an annual completing its life-cycle in one season. Its height is from 30–60 centimetres, and the first inflorescence is terminal, no branching occurring until the flower is over. The inflorescence is white, tinged with blue, and bears from one or two to ten florets, and scarcely ever exceeds 8 centimetres in height. As soon as the first inflorescence is over, lateral buds grow out from the axils of the upper two or three leaves and these in turn produce inflorescences, whose withering is followed by similar growth of lateral shoots. The whole plant dies at the end of the season.

Lupinus polyphyllus (variety Waterer's Sunshine) is a herbaceous perennial which does not habitually flower until the second season. At the beginning of the second season the plant consists of a thick rootstock and short axis on which the leaf-bases of the previous year closely overlap one another. The first leaves which develop on the second-year plant are large and have long petioles. Their growth is followed by shoots 60–120 centimetres high which terminate in inflorescences. The inflorescence is bright yellow and grows to a height of 25–35 centimetres. After flowering, leafy shoots grow out on the flower branches, the whole of which die down in autumn.

Lupinus arboreus (variety Sutton's yellow) is a woody shrub about 180 centimetres in height. This also does not flower until the second year. The flowers are bright yellow and the inflorescences are always terminal. When fully out, the inflorescence attains a height of eighteen centimetres and bears florets in eight or nine whorls. After flowering, the shoots in the axils of the leaves on the flowering stems, which have remained short hitherto, grow up very rapidly, so that the plant is soon covered with fresh leafy shoots. These constitute the new woody part of the shrub and only some of the leaves are shed in autumn.

Previous work has been recorded for the seedlings of many species, e.g. Czapek (1898), Fitting (1905), Bach (1907), Brain (1926), Hawker (1932); also for inflorescence axes, e.g. Fitting (1905), Bach (1907); and fern-fronds, e.g. Prankerd (1925, 1929), Waight (1923).

Dr. Prankerd first suggested that a study of the gravitational irritability of one species of plant, at different stages of its development, might yield

2 E 2

interesting results. The experiments recorded below have been performed on three species of *Lupinus*, so that the course of sensitivity, as measured by the presentation time, can be traced in each individual and the behaviour of the different species compared.

METHODS

The experiments with seedlings have been carried out by the method fully described in my previous paper (Brain 1926). They were performed in a research greenhouse at 20° C. $\pm$ 1° and 70–90 per cent. humidity. Experiments with the inflorescences and later internodes of *L. albus* were performed in the greenhouse. But as the plants of *L. polyphyllus* and *L. arboreus* were growing in the garden experiments on them were performed out of doors, at a temperature as near 20° C. as possible. Records of the growth of the plants were kept previous to and following experimentation.

The upright method of stimulation was always used, seedlings and plants in pots being placed horizontal for the required length of time and then replaced upright. Inflorescences of *L. polyphyllus* and *L. arboreus* were stimulated by being bent horizontal as far below the inflorescence as was possible. The inflorescences were supported underneath to prevent sagging, and were kept in position by tying to the support.

The presentation time has been taken as the minimum length of stimulation which will produce a responsive movement of about 5°–10° in 80 per cent. of the plants used (cf. Prankerd 1929, Brain 1926). The angles were measured with a transparent protractor. The latent time, as recorded below, represents the time elapsing between the beginning of stimulation and the first movement which is visible to the naked eye.

The following abbreviations have been used :—P.T.=presentation time ; L.T.=latent time ; P.S.=period of stimulation.

SEEDLING RESULTS

a. ONTOGENY OF GRAVIPERCEPTION.

The seedling of *L. albus* has been used for a detailed examination of the ontogeny of graviperception and response.

The following results were obtained for the radicle.

TABLE I.—*Radicle of* L. albus.

Length, in cm.	P.T., in mins.	L.T., in mins.	Average growth per day, in cm.
·5–1·0	80	120	·37
1·0–2·0	40	92	1·26
2·0	25	70	2·26

Text-fig. 2 shows that the graviscripts * for the P.T. and L.T. are approximately parallel.

* A graviscript was used by Prankerd (1929) and defined as a curve ' where the ordinates are the presentation times (or latent times), and the abscissae the periods intervening between the stages.'

Previous workers, e.g. Schultze (1910), Copeland (1901), have cited ' positive geotropism ' in the hypocotyl of *L. albus*. However, they do not seem to have taken into account the fact that in early stages of growth the hypocotyl and radicle are not clearly differentiated, so that curvatures which are spoken of as positive in the hypocotyl are really positive curvature in the radicle (text-fig. 1).

In seedlings under 3·0 cm. from cotyledons to root-tip, continuous stimulation will produce a positive geotropic response only—the basal portion of the hypocotyl being involved in the curvature. Older seedlings, in which the hypocotyl

TEXT-FIG. 1.
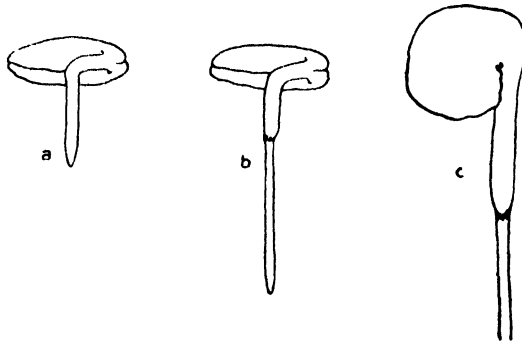
L. albus seedling. *a*. Radicle+hypocotyl 1·5 cm, shows positive geotropism only. *b*. Radicle 2·0 cm, shows positive geotropic response; hypocotyl 1·0 cm., shows no geotropic response. *c*. Hypocotyl erect, 2·0 cm., shows negative geotropism.

is well defined, but under 1·5 cm. in height (text-fig. 1, *b*), will show a positive curvature in the radicle, but no response at all to continuous stimulation in the hypocotyl. Hypocotyls above 1·5 cm. in height (text-fig. 1, *c*) do show negative response on continuous stimulation, but it has not been possible to determine the P.T., as the growth-rate is very slow—0·1 cm. per day (see p. 379).

The P.T. and L.T. have been obtained for different stages of hypocotyls above 1·8 cm., the results being recorded in Table II.

TABLE II.—*Hypocotyl of* L. albus.

Length, in cm.	P.T., in hours.	L.T., in hours.	Average growth per day, in cm.
2·0	3·5	5	·4
2·5	2·35	3	·6
3·0	1·5	2	·9
3·5	1·0	1·5	1·0
4·0	·5	1·5	1·5
4·5	·33	1·33	1·5

Above 4·5 cm. in height the P.T. for the hypocotyl remains constant at twenty minutes until the epicotyl appears and the hypocotyl ceases to grow. I have not been able to detect a rise in value for the P.T. as referred to by
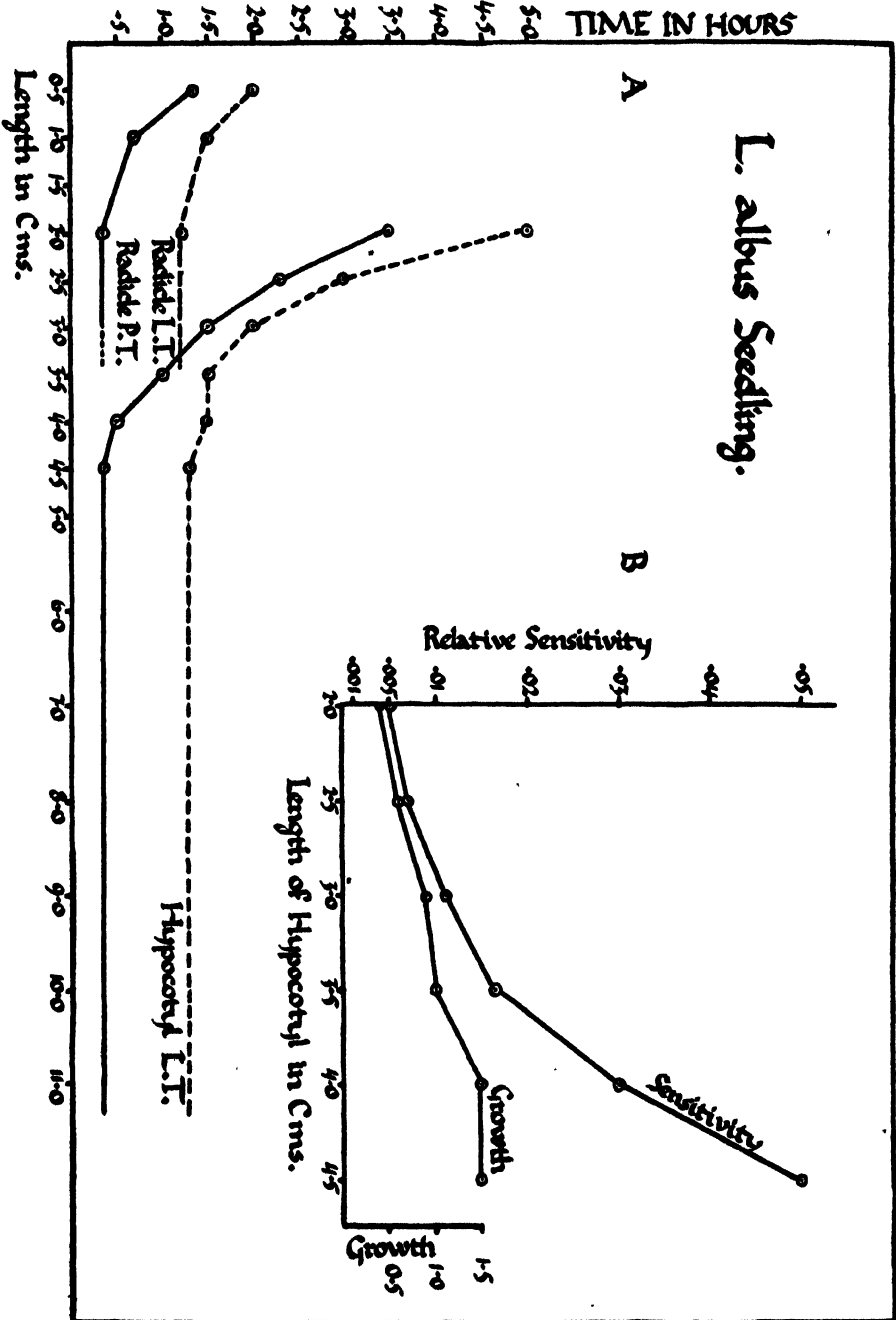
a. Graviscripts for P.T. and L.T. at 20° C. for *L. albus* hypocotyl and radicle. b. Graph
to show the relation between sensitivity to gravity and rate of growth of hypocotyl.
Relative sensitivity to gravity is shown by plotting the reciprocal of the P.T. for each
stage.   In both graphs stage is represented by different lengths of hypocotyl and radicle.

Hawker for various seedlings (Hawker, 1932, p. 154). Hypocotyls of *L. albus* either respond to a stimulus of twenty minutes or will not respond at all.

In text-fig. 2 it will be seen that the graviscripts for the P.T. and L.T. of the hypocotyl are more or less parallel, and as for the radicle the P.T. and L.T. fall in value as the seedling grows in length until a constant time is reached.

b. Epicotyl and first internodes of *L. albus*.

When dealing with epicotyls and the successive internodes of the plant it was found necessary to watch the growth of the plants used for each series of experiments, for as the successive nodes develop there are successive pauses in the growth-rate when response to the P.T. for the internode at its maximum growth will not occur. When calculating the P.T., therefore, the plants which showed a growth-rate of less than ·2 cm. on the day of experiment were not included in the results. For epicotyls P.T.=20 mins., L.T.=65 mins.

The ontogeny of graviperception exhibited in *L. albus* seedlings is also evident in those of *L. polyphyllus* and *L. arboreus*, but the P.T. for the different stages has not been accurately worked out for the latter species. It has been found that radicles and hypocotyls under 1·0 cm. of both species require a stimulus of more than one hour to produce any visible response.

Table III. gives a classified record of the results of experiments on the three species of seedlings.

TABLE III.—*Seedling results.*

P.S., in mins.	Length, in cm.	Number of experiments.	Percentage response.	Average angle of curvature.	Average L.T.	Average growth per day, in cm.
L. albus radicle :						
90	·5–1·0	9	88	30°	115	·37
80	....	15	80	10°	120	....
60	....	14	50	11°	96	....
40	1·0–2·0	23	82	11°	92	1·26
35	....	18	72	11°	92	....
25	2·0	8	87	7°	70	2·26
20	....	25	64	12°	71	....
L. albus hypocotyl :						
255–360	1·5	13	—	—	—	·1
210	2·0	8	100	6°	300	·44
200	....	8	25	10°	300	....
150	2·5	3	100	11°	180	·57
140	....	9	100	7°	180	....
120	....	5	60	4°	170	....
90	3·0	6	83	8°	120	·9
80	....	6	66	10°	170	....
80	3·5	4	100	10°	150	1·0
60	....	6	100	12°	90	....
50	....	5	60	8°	80	....
40	4·0	11	81	7°	96	1·49
30	....	6	100	11°	90	....
20	....	14	57	6°	90	....

TABLE III (cont.).

P.S., in mins.	Length, in cm.	Number of experiments.	Percentage response.	Average angle of curvature.	Average L.T.	Average growth per day, in cm.
L. albus hypocotyl (*cont.*) :						
25	4·5	13	85	8°	85	1·5
20	....	71	87	8°	80	....
15	....	20	15	6°	80	....
L. albus epicotyl and first internodes :						
25	·5	13	84	16°	101	·4
20	....	64	80	7°	65	....
15	....	10	40	7°	45	....
L. polyphyllus radicle :						
20	1·0	17	76	10°	45	1·0
15	....	10	10	5°	45	....
L. polyphyllus hypocotyl cotyledonary plane :						
20	1·0	31	87	8°	59	·7
15	....	8	12	10°	43	....
Intercotyledonary plane :						
80	1·0	22	82	11°	103	....
75	....	16	44	7°	112	....
60	....	27	44	10°	100	....
20	....	21	....	....	....	....
L. arboreus radicle :						
20	1·0	18	78	10°	39	1·0
L. arboreus hypocotyl cotyledonary plane :						
20	1·0	12	83	10°	52	·4
15	....	9	36	5°	52	....
Intercotyledonary plane :						
60	1·0	7	85	7°	105	....
40	....	5	20	10°	120	....
L. arboreus epicotyl and first internodes :						
20	·5	13	77	5°	52	·3
15	....	17	41	5°	52	....

(Deduced P.T.s are printed in **Clarendon**.)

COMPARISON OF THE BEHAVIOUR OF THE THREE SPECIES OF SEEDLING.

Physiological zygomorphy.

The seedlings of *L. polyphyllus* and *L. arboreus* are similar in size and shape and more slender than the large fleshy seedling of *L. albus*. Their behaviour in response to geotropic stimulation also differs in some respects from the response of *L. albus* seedlings. In a previous paper instances were recorded of seedlings which showed bilateral symmetry in their response to stimulation in the cotyledonary and intercotyledonary planes of the hypocotyl and which were termed 'physiologically zygomorphic.' *L. polyphyllus* was one of the examples used as a physiologically zygomorphic seedling and *L. albus* as a physiologically

radial one, having the same P.T. for both planes of the hypocotyl. *L. arboreus* is also physiologically zygomorphic, having a P.T. of twenty minutes for the cotyledonary plane and sixty minutes for the intercotyledonary plane of the hypocotyl.

It is of considerable interest to note that Hawker in her recent paper on seedlings puts forward a complete explanation of the phenomenon of bilateral symmetry on the basis of the statolith apparatus of the seedling.

Seasonal variation.

L. polyphyllus and *L. arboreus* also differ from *L. albus* in showing variation in response to geotropic stimulation at different times of year. *L. albus* responds equally in winter and summer months, but *L. polyphyllus* and *L. arboreus* differ in this respect. *L. polyphyllus* has a high percentage of germination all the year, but shows a distinct decline in response to gravity in the winter months, although the growth-rate remains constant. *L. arboreus* has not been effectually germinated between November and March, and figures for November show a lower percentage response than in March, although the growth-rate is practically identical. The results are recorded in Table IV.

TABLE IV.—*Seasonal variation in response of* L. polyphyllus *and*
L. arboreus *hypocotyls.*
Stimulated in the cotyledonary plane for the P.T. (20 minutes)
epicotyl and first internodes.

	Growth per day, in cm.	Percentage response.	Growth per day, in cm.	Percentage response.
	L. arboreus.		*L. polyphyllus.*	
January	....	....	·67	30
February	....	....	·95	47
March	·34	83	·66	75
April	....	....	·6	86
June	....	....	1·2	87
November..........	·35	0	·66	31·5
December	....	....	·35	4

In *L. polyphyllus* the epicotyl and first internodes grow so slowly and the leaves so closely overlap one another that the P.T. and L.T. were not determined.

The P.T. for the first internodes of *L. arboreus* is 20 minutes and the L.T. is 52 minutes. These are the same as the P.T. and L.T. for the radicle and cotyledonary plane of the hypocotyl of *L. arboreus*.

RESULTS FOR INFLORESCENCES AND LATER INTERNODES

· As the graviperception of inflorescences seems to be influenced by the stage of development of the inflorescence at the time of experiment, it was found necessary to classify the inflorescences according to the condition of the latter rather than merely by height-measurements.
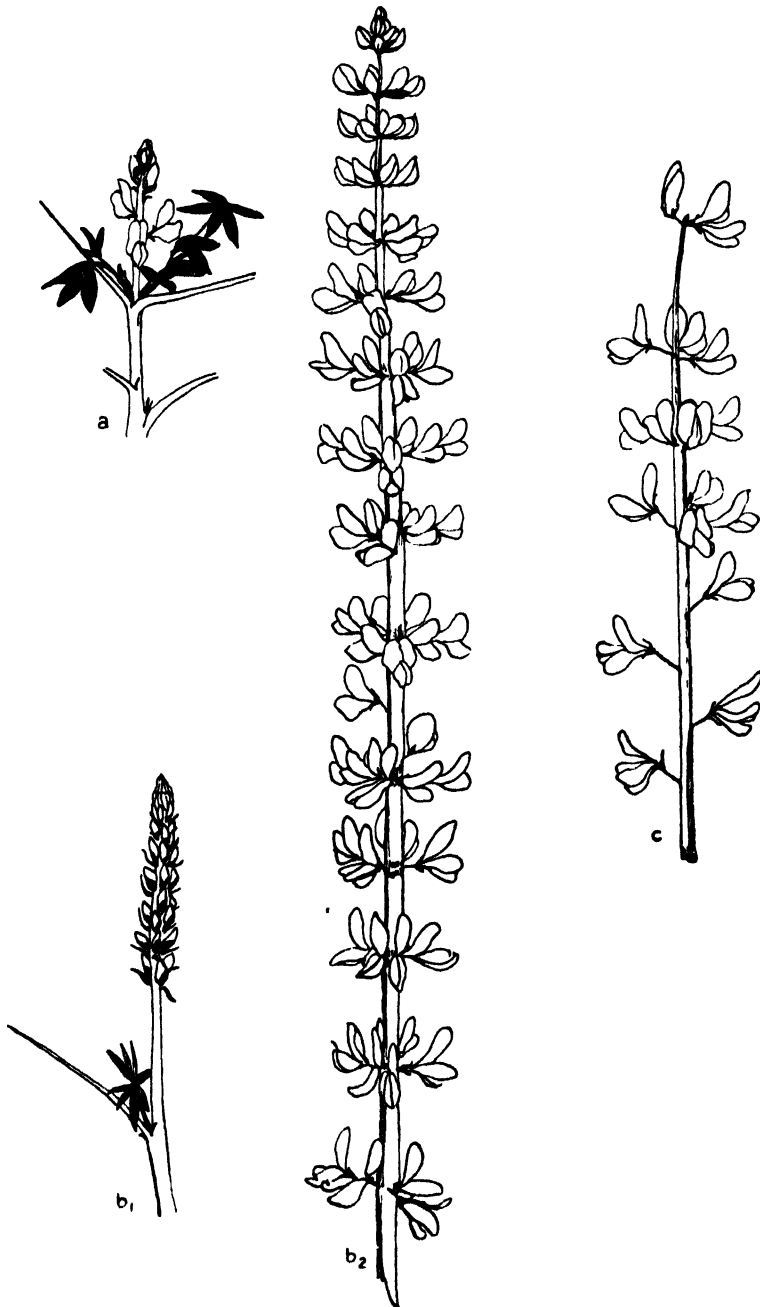
Inflorescences of the three species of *Lupinus* at their most sensitive stages. *a. L. albus.* Stage A. P.T.=2·5 minutes. b_1. *L. polyphyllus,* Stage B. b_2. *L. polyphyllus,* Stage A. (P.T. throughout both stages is 5 minutes.) *c. L. arboreus,* Stage A. (P.T. 20 minutes.)

Classification has therefore been arranged as follows :—

Stage B' : all florets in close green buds.

Stage B : all in bud, showing colour of petals.

Stage A : florets open fully in lowest whorl.

Stage A† : florets withering, growth ceasing.

Measurements have been taken for recording the growth-rate of peduncles and growth-rate and height of inflorescences. Heights of inflorescences have been measured from the base of the lowest pedicel to the tip of the inflorescence.

The ontogeny of graviperception has been traced in the young plant of *Lupinus albus*. Similar phenomena occur in the developing inflorescence, as the results recorded below will demonstrate. (See Table V. & VI.)

TABLE V.—*Classified results for inflorescences and later internodes of three species.*

P.S., in mins.	Stage and length, in cm.	Number of experiments.	Percentage response.	Average angle of curvature.	Average L.T., in mins.	Average growth-rate per day, in cm.
L. albus :						
20	Preinflorescence.	21	81	9°	74	·93
15	,,	7	42	10°	75	....
10	,,	19	21	10°	75	....
20	{ Inflorescence B' under 2·0. }	63	79	10°	80	·73
15	,,	32	28	10°	66	....
10	,,	61	30	9°	66	....
10	B over 2·0.	16	94	10°	65	2·0
5	,,	17	88	7°	54	....
2·5	,,	28	50	9°	47	....
3	A 2·0–8·0.	9	100	7°	59	1·2
2·5	,,	11	82	7°	65	....
2	,,	12	50	9°	53	....
10 } 5 }	Later internodes and inflorescences.	{ 28 { 40	88 33	6° 6°	52 55	·48 ....
L. polyphyllus :						
10	{ Over 4·5 B and A stage. }	5	80	9°	55	1·6
5	,,	12	91	18°	55	....
2·5	,,	8	25	3°	75	....
L. arboreus :						
20	{ 1st year internodes. }	25	84	11°	68	·9
15	,,	9	44	10°	79	....
120	B' under 3·0.	25	75	10°	180	1·0
90	,,	7	30	12°	150	....
40	B 3·0–6·0.	7	100	12°	75	·66
30	,,	9	77	15°	70	....
20	,,	15	60	9°	69	....
20	A 6·0.	20	85	9°	50	1·6
15	,,	15	30	7°	59	....
20	{ Later internodes after flowering. }	29	79	7°	65	·8
15	,,	10	50	12°	57	....

(Deduced P.T.s are printed in **Clarendon**.)

Inflorescences.

L. polyphyllus

L. arboreus

L. albus

Length in Cms.

Stages, and Time in Days

Relative Sensitivity
Growth Rate
⊙ L. albus
• L. polyphyllus
△ L. arboreus

Relative Sensitivity

Growth in Cms. per day

B, Stages   B   A
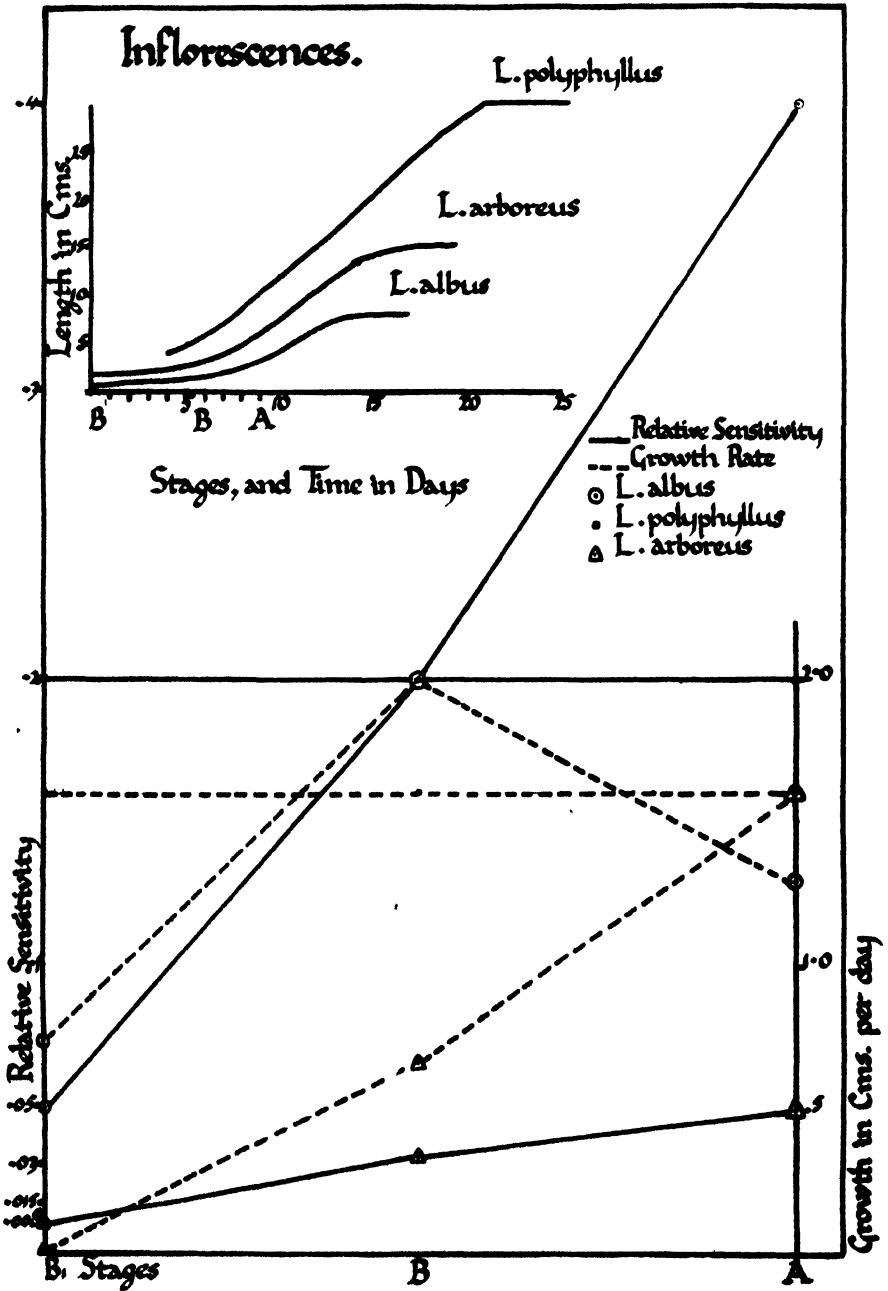
Graphs to show the relationship between sensitivity to gravity and stage of development
of inflorescences in the three species. Relative sensitivity is shown by plotting
the reciprocal of the P.T. at each stage. The inset shows the specific differences of
length at each stage.
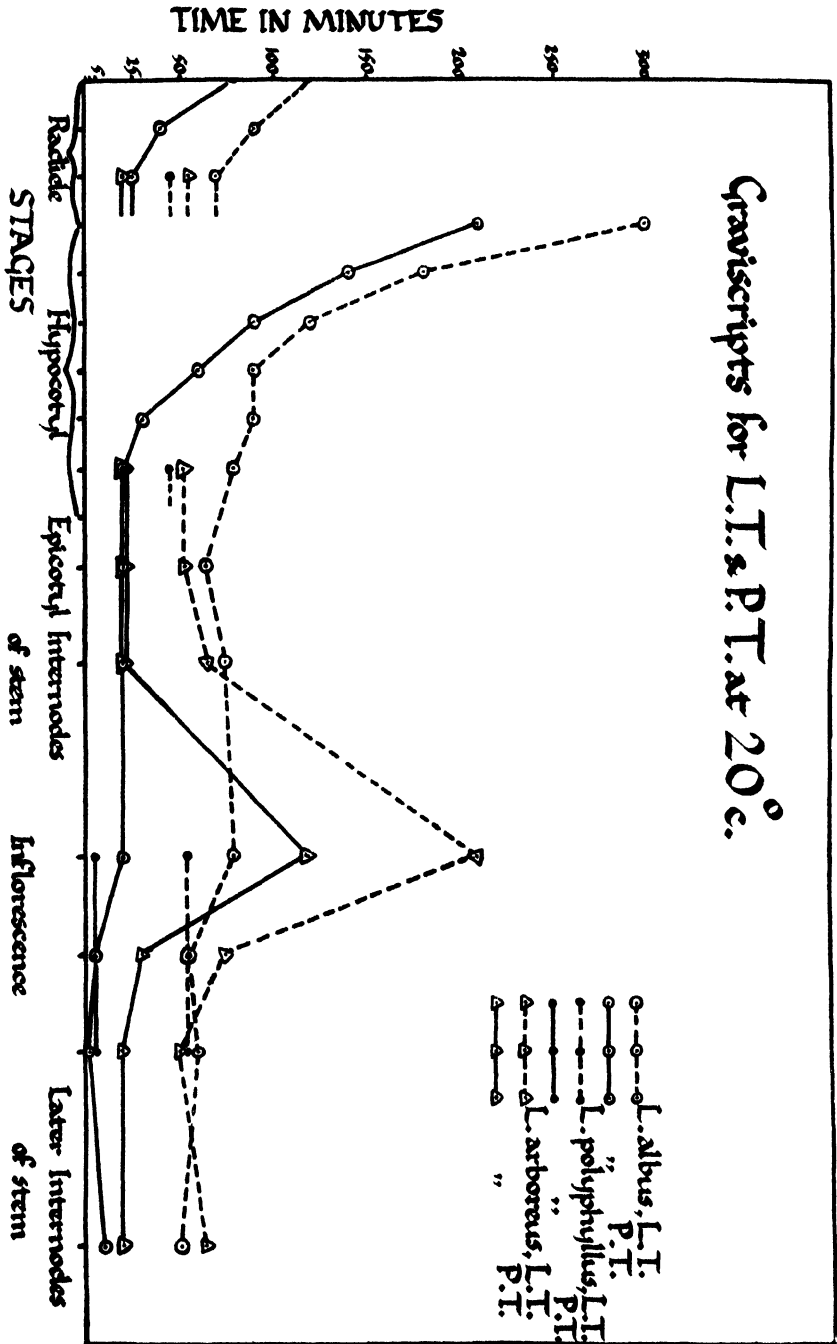
Graviscripts for P.T. and L.T. for the three species at 20° C., which illustrate the variations in sensitivity at the different stages of the plant.

COMPARISON OF BEHAVIOUR OF INFLORESCENCES AND LATER INTERNODES OF THE THREE SPECIES.

The most striking point which is brought out in the results of these experiments is the variation which occurs in the P.T. for the inflorescence of the three species. Here again, as in the seedlings, a comparison must be made between the most sensitive stages in each. This is stage A for *L. albus* when the P.T. is 2·5 minutes, stage B and stage A for *L. polyphyllus* when the P.T. is 5 minutes, and stage A in *L. arboreus* when the P.T. is 20 minutes. The P.T. of 20 minutes holds good for the inflorescences and later internodes of *L. arboreus* as for the seedling, but there is an increase in sensitivity in the inflorescences and later internodes of *L. albus* and the inflorescences of *L. polyphyllus*. This is very marked in *L. albus*, which is eight times more sensitive in the A stage than *L. arboreus* at the same stage. (See text-fig. 3, p. 382.)

As the inflorescences develop the zone of greatest growth in *L. polyphyllus* and *L. arboreus* travels towards the tip. In *L. albus* the peduncle below the inflorescence has a greater growth-rate even in the A stage ; whereas in the other two species growth ceases in the peduncles before the A stage is reached. However, in the three species, curvature occurs below the inflorescence in the B' stage, and as the inflorescences develop the part involved in curvature becomes nearer the tip. In the B stage the tip often curves more than the lower part. *L. polyphyllus* has the same P.T. for the B and A stages, but for the same period of stimulation it shows progressively decreasing angles of curvature as the inflorescence develops.

In text-fig. 4 the relation between stage of inflorescence, sensitivity to gravity, and growth-rate is shown.

In the graph the relative sensitivity to gravity is the curve obtained by plotting the reciprocals of the P.T.s at the different stages (Hawker, 1932, p. 128). It will be seen that for *L. albus* and *L. arboreus* this does not bear any definite relation to the growth-rate, but for *L. polyphyllus* growth-rate and relative sensitivity are parallel lines. The specific differences of sensitivity to gravity are very marked, and the fact that specific differences of height do not affect sensitivity is clearly shown by comparing the graphs.

Nor does the height of the individual inflorescence affect the graviperception so much as its stage. This is especially noted in *L. albus*, of which inflorescences of 1·5–2·0 cm. bearing two or three florets respond as readily as inflorescences of 8 cm. (cf. Waight (1923) for fronds of *Asplenium bulbiferum*).

In conclusion, the table of P.T.s and L.T.s for the three species and text-fig. 5 bring out the following facts :—

(1) The similarity of *L. polyphyllus* and *L. arboreus* in the seedling stage, both showing physiological zygomorphy and seasonal variation in response to gravity and the difference from *L. albus* in these respects.

(2) The increase of sensitivity from the seedling to the inflorescence stage in both *L. albus* and *L. polyphyllus*. This contrasts with *L. arboreus*, in which the maximum sensitivity is the same at both seedling and inflorescence stages,

(3) The L.T. is less variable than the P.T. at the different stages in the three species. This corresponds with results found for Pteridophyta (cf. Waight, 1923, and Prankerd, 1929).

TABLE VI.—*P.T. and L.T. for the three species.*

	L. albus.		*L. polyphyllus.*		*L. arboreus.*	
	P.T., in mins.	L.T., in mins.	P.T., in mins.	L.T., in mins.	P.T., in mins.	L.T., in mins.
Radicle :						
	25	70	20	45	20	52
Hypocotyl :						
	20	80	20	59	20	52
	....	....	80	103	60	105
Epicotyl :						
	20	65	....	....	20	52
Inflorescence :						
B′	20	80	....	....	120	210
B	5	54	5	55	30	70
A	2·5	59	....	....	20	50
Later internodes :						1st year : 20 → 68
	10	52	....		Later : 20	65

DISCUSSION OF RESULTS

There are one or two observations of general significance arising out of the results of these experiments.

Firstly, the effect of growth-rate on geotropic response. It has been stated (see page 386) that the geotropic sensitivity as measured by the P.T. is not directly dependent on growth-rate, but is a specific character of the plant ; but it has been found in the seedling and later stages of the plant that if the growth-rate is less than ·2 cm. on the day of experiment, responsive movement to a stimulus equivalent to P.T. for plants of average growth rate rarely (if ever) occurs, which seems to indicate a minimum growth-rate below which response of any individual plant to P.T. does not occur. Results recorded in Tables I and II show that in *L. albus* seedlings, L.T. decreases in direct proportion to increase in growth-rate. In the later stages of the plant the same relation does not appear to hold (Table V). The growth-rate does not seem to affect the amplitude of movement.

Secondly, the angle of curvature rises with an increase in the length of stimulus when the period of stimulation is longer than the P.T. For periods shorter than the P.T. at any given stage of the plant, the percentage of plants used which respond is less for the shorter stimulus, but the angle of curvature is not appreciably lessened. Whereas by increasing the stimulus above the length of the P.T. at any given stage, the percentage of plants which respond is not greatly increased above 80 per cent., but the angle of curvature is increased as a result of the increase in stimulus.

These results fall into line with those of Lundegårdh, who stated (1928) that the reaction optimum depends on the quantity of stimulation, and that a simple reaction effect is proportional to the stimulus given.   Maurice Rose in ' Les Tropismes ' (1929) also states that if one varies the length of the stimulation the L.T. does not alter, but intensity of reaction is modified.

Using different quantities of centrifugal force for varying the intensity of stimulation, Bach (1907) has shown also that L.T. does not vary in any corresponding degree.

Previous mention has been made of the greater variability of P.T. than L.T. at different stages in the three species.   A possible explanation of specific differences of sensitivity (Table VI) and of the seasonal variation exhibited in seedlings of L. polyphyllus and L. arboreus lies in the biological factor of specific differences of life-habit.

With regard to the physiological zygomorphy of the hypocotyls of L. polyphyllus and L. arboreus and the radial behaviour of L. albus, it is interesting to note that Holden (1925) arranges the lupines in a series according to their vascular anatomy which he regards as being one of evolutionary sequence, with L. albus at one end and L. arboreus and L. polyphyllus towards the other. If this is so, even though the physiologically zygomorphic tendency is due to zygomorphic structure, it seems interesting that it may be associated with a higher type of seedling and that possibly the radial behaviour is primitive and the zygomorphic derived.   It does seem apparent that the P.T., or degree of gravitational irritability, is a specific character of the plant.   Also that it is modified by the development of the individual and correlated with the life-habit of the species.

SUMMARY OF RESULTS.

I. A comparison between three species of Lupinus has been made, based on over one thousand experiments.

II. An ontogeny in graviperception has been traced in the seedlings of each species—also in the inflorescences of L. albus and L. arboreus.

III. L. arboreus and L. polyphyllus seedlings show similarities in behaviour, both species being physiologically zygomorphic and exhibiting a seasonal variation in their gravitational irritability.

IV. The shortest P.T. for the three species in the seedling is twenty minutes. L. arboreus does not show the increase in sensitivity in the inflorescence which L. albus, with two and a half minutes, and L. polyphyllus, five minutes, exhibit.

V. Sensitivity to gravity is dependent on the stage of the inflorescence rather than length.   It is also not directly dependent on growth-rate.

VI. As in certain ferns the L.T. has been found to be a more constant quantity than the P.T. in the three species.   Both L. polyphyllus and L. arboreus have a shorter L.T. for the radicle than at any other stage and differ

from *L. albus*, which has a shorter L.T. for the inflorescence-stages than for the seedling.

VII. Specific differences in the P.T. are marked in the inflorescence-stages of the life-cycle. The biological factor of life-habit is put forward as a possible explanation of these divergences.

I wish to acknowledge with grateful thanks the helpful advice and interest which I have received from Dr. T. L. Prankerd.

University of Reading.

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Scientific results of the Cambridge Expedition to the East African Lakos,
1930-1.—7. The Algae.   By FLORENCE RICH, M.A., F.L.S.

(With 4 Text-figures)

[Read 2 February 1933]

[This paper was published in Journ. Linn. Soc., Zoology, xxxviii (No. 259),
pp. 249-275, on 26 April 1933.]

A revision of *Lobostemon* Lehm., and a discussion of the Species Problem. By Margaret R. Levyns. (Communicated by Edith L. Stephens, B.A., F.L.S.)

(Plate 29, and 16 Text-figures)

[Read 6 April 1933]

Lobostemon has long been recognised as a difficult genus, and it has been almost impossible to make specific identifications in the field. During a number of years I have been engaged in studying the vegetation of the south-western Cape, with special reference to the western borders of the karoo. Among plants collected were several Lobostemons, and many fruitless attempts were made to name these with the keys and descriptions in the available literature. Finally, it became obvious that whereas the plants collected could be separated from one another by good recognisable characters in the flower, such characters were hardly mentioned in existing works. A revision of the whole genus seemed imperative, and the work was started in 1926.

During the course of the investigation I have received generous help from many institutions and persons, and it gives great pleasure to acknowledge my indebtedness. Sir Arthur Hill, Director of the Royal Botanic Gardens, Kew, granted me the invaluable privilege of using the Herbarium and Library during a stay of six weeks at Kew. In addition, through his assistance, I was enabled to obtain on loan specimens from Berlin, Vienna, Uppsala, Geneva, Zürich, and Paris, and to Dr. Diels, Dr. Keissler, Professor Svedelius, the late Dr. John Briquet, Dr. Däniker, and Professor H. Lecomte, of the various institutions in the places mentioned above, my warmest thanks are due. To Mr. A. D. Cotton, Keeper of the Herbarium, Kew, Mr. J. Hutchinson, and Mr. Skan I owe much for their kindness and help. Through the courtesy of Mr. J. Ramsbottom, Keeper of the Department of Botany, British Museum, I was able to examine the collection housed there. I am grateful for the permission afforded me by Mr. S. Savage, Librarian and Assistant Secretary of the Linnean Society, to examine the plants in Linné's Herbarium. Professor Seward kindly granted me facilities for going through the herbarium material in the Botany School at Cambridge. To Mrs. L. Bolus, Curator of the Bolus Herbarium, and Dr. L. Gill, Director of the South African Museum, I am indebted for the loan of herbarium material and many other facilities. I am grateful to Dr. I. B. Pole Evans, Chief of the Division of Plant Industry, Mr. R. A. Dyer, Curator of the Herbarium in the Albany Museum, the late Dr. R. Marloth, and the late Professor C. E. Moss for the loan of specimens,

HISTORICAL NOTE

The genus *Lobostemon* was founded by Lehmann in 1830 on a specimen grown in the Botanic Gardens at Hamburg, named by him *Lobostemon echioides*. In distinguishing this genus from *Echium* and other related genera, Lehmann emphasised the possession of a scale-like outgrowth at the base of the stamens. In 1837 Buek transferred to *Lobostemon* thirty-two South African species, most of which had been included formerly in *Echium*. He extended Lehmann's genus to include certain species in which staminal scales were absent, but in which hairs were present on the lower parts of the filaments. In considering Buek's work, which was carried out entirely on herbarium material, and at a time when the dogma of the constancy of species influenced all systematic work, one cannot but be amazed at the excellence of his account. His strong feeling for affinity led him to group the species in a phylogenetic series, and if later workers had appreciated Buek's almost uncanny insight into the inter-relationships of these species much confusion would have been obviated.

In 1846 de Candolle gave an account of the genus, to which several new species were added, but all those species without definite scales were replaced in the genus *Echium*. This in itself was not a retrograde step, but in de Candolle's general grouping Buek's insight into the true relationships of the species was obscured. By the emphasis which he placed on vegetative features and the neglect of floral structure, he laid the foundations of much of the confusion that has existed since his time.

De Candolle's arrangement was closely followed by C. H. Wright in the ' Flora Capensis '. In one respect Wright reverted to Buek's earlier conception of the genus in that once more those forms without scales (with the inexplicable exception of the plant termed by him *Echium formosum* Pers.) were returned to the genus *Lobostemon*. The key to the species given in the ' Flora Capensis ' was based mainly on the relative size of the inflorescence and on the size and hairiness of the leaves. Field-knowledge of the genus has shown that these characters exhibit variability of a high order, a phenomenon which will be discussed at length later. Since the publication of the ' Flora Capensis ' nothing of importance has been added to our knowledge of the genus.

In the present work it will be shown that, using floral characters, the genus falls into natural sections which Buek tacitly foreshadowed in his grouping of the species.

Buek recognised thirty-three species, de Candolle forty species of *Lobostemon* and eleven additional species which he placed in *Echium*. C. H. Wright described fifty-three species in *Lobostemon*, and if to these we add three tropical African species (19), one named by N. E. Brown (6) and one by Schinz (16), the total is brought up to fifty-eight.

As a result of the present investigation this number is found to be far too high. It is proposed to remove from *Lobostemon* a small section containing three species and to constitute a new genus, *Echiostachys*, for these. *Lobostemon* in the present restricted sense contains only twenty-eight species.

DEFINITION OF LOBOSTEMON AND ECHIOSTACHYS

Lobostemon is an advanced member of the Boraginaceae, closely allied to *Echium*, in which genus it was included when the Cape plants were first discovered. At the present day any one of the definitions of *Lobostemon* given in standard works on taxonomy will exclude some of the species which rightly belong to the genus.

A careful study of plants in the field and of herbarium specimens shows that under *Lobostemon*, as at present constituted, two distinct groups may be recognized. In the first, to which I propose to restrict the name *Lobostemon*, the plants are usually shrubby. In two species the habit is almost herbaceous, but the aerial stems are woody at the base and the leaves arise in the usual way on the aerial stems. In this group a densely hairy scale, ridge, or protuberance is always present at the base of the stamens. The second group, which I propose to separate as a new genus, *Echiostachys*, is herbaceous in habit, with tufts of leaves arising annually from an underground stem. The inflorescence has a bottle-brush appearance, superficially quite unlike that of any true *Lobostemon*, and, although hairs are present towards the lower ends of the filaments, there is never a true scale or definite swelling at the bases of the stamens.

The stamens with their well-developed filaments and subglobose anthers are characteristic features of both *Lobostemon* and *Echiostachys*.

Baker and Wright, in the ' Flora of Tropical Africa ' (19), record three species of *Lobostemon* from that region. Two of these, *L. somalensis* Franchet and *L. lithospermoides* Baker, had previously been described by Spencer Moore as species of *Leurocline* (17), a genus in which amongst the diagnostic features are given a definitely two-lipped tubular corolla and stamens with very short filaments. No true *Lobostemon* has these characters, and, when the entire absence of a hairy scale or swelling at the base of the stamens is added, it is obvious that these two species have no claim to be regarded as Lobostemons. The third species given by Baker and Wright is *L. cryptocephalum* Baker (3).

I have seen Baker's specimen, and can find no justification for its inclusion in *Lobostemon*. It has a narrow corolla unlike that of any *Lobostemon*, there are no hairy scales or lumps at the base of the stamens, the filaments are short, and the anthers are long and pointed at one end.

The removal of these tropical species from *Lobostemon* leaves the genus confined to southern extra-tropical Africa.

FEATURES OF LOBOSTEMON Lehm.

So little has been written about the floral structure in *Lobostemon* that a full account of it seems desirable. The range of floral structure exhibited is considerable, but an orderly grouping is revealed on a comparative examination.

The family Boraginaceae, as a whole, is characterised by regular flowers and cymose inflorescences, and it is therefore legitimate to assume that where zygomorphism occurs, or where the inflorescence is apparently not cymose, we are dealing with relatively advanced forms. The section to be described first may, for convenience, be regarded as the primitive one from which all the other groups have diverged, although the possibility should be kept in mind that this, like all other evolutionary series, may receive other interpretations.

As a preliminary to the discussion of the different sections a brief statement of the characteristic features of the genus as a whole will be of use. The inflorescence (except in Section III. ARGENTEI) consists of a number of unilateral cymes, which are usually racemosely arranged. These are more or less congested when young, but elongate greatly in the fruiting stage, so that the appearance of the plant varies with its stage of development. Each flower is associated with a leaf-like bract, which is frequently large at the base of the cyme, but shows a progressive diminution in size and a strong tendency to become asymmetrical. The flowers may be regular, zygomorphic, or occasionally asymmetrical. Zygomorphism is the most common condition, and the plane of symmetry is oblique, as is usual in the family. The flowers are 5-merous, and as all whorls are variable these will be discussed under each section. The gynoecium is the most stable organ. Hairs in the style are present in some sections and absent in others, but apart from this feature the gynoecium offers no characters of diagnostic value. The fruit is characteristic of the different sections.

L. echioides Lehm., the original species in the genus, may be taken as typical of Section I. ECHIOIDES. The inflorescence shows a marked degree of elongation in the fruiting stage, the phenomenon attaining its maximum development in this section. Failure to recognise this has led to much confusion in the past. For instance, specimens of *L. paniculatus* Buek, collected at Ladismith in July, showed inflorescences with a maximum diameter of 2·5 cm. Specimens collected from the same plant three months later showed inflorescences with diameters as great as 18 cm. (Pl. 29). I have quoted measurements taken from *L. paniculatus* rather than from *L. echioides*, as this is the only

species in which collections were made *from the same plant* at different seasons, but equally good illustrations could be obtained from *L. echioides*. In this section the bracts are relatively smaller than in the other sections. The flowers, too, are small, being about 1 cm. in length or less. The flower is regular, possessing equal calyx-lobes, free almost to the base, and a corolla of the type shown in text-fig. 1. The base of the corolla forms a cylindrical tube, which at a point about half-way up suddenly expands, so that the lobes spread abruptly outwards.

TEXT-FIG. 1.
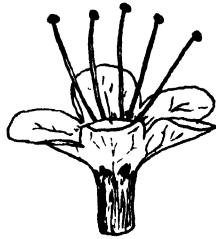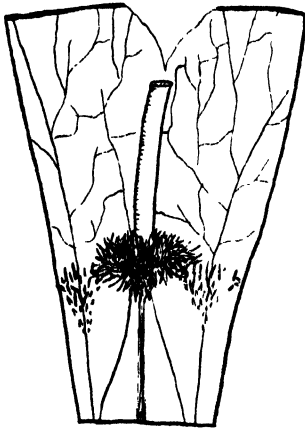
TEXT-FIG. 2.   TEXT-FIG. 3.
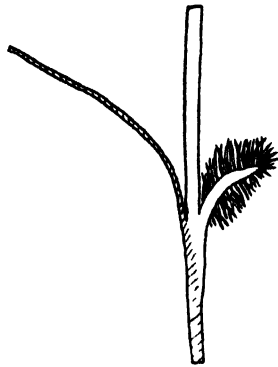
Lobostemon echioides.

Fig. 1.—External view of corolla and stamens.   × 3.
Fig. 2.—Front view of staminal scale.   × 6.
Fig. 3.—Longitudinal section of the corolla, showing the scale in section.   × 6.

The outer surface is usually hairy. The scales which envelope the bases of the stamens are well developed and placed in the throat of the corolla, so that they are clearly visible without dissecting the flower. Text-figs. 2 & 3 show the scale in front view and in section respectively. It will be seen that the scale is densely hairy and bends towards the centre of the flower, almost blocking the space between the style and the corolla. The stamens are equal or nearly so, become

free from the corolla immediately above the scales, and are much exserted. Each nutlet is somewhat pointed at the apex.

Within this group, apart from differences in the size of the corolla, only minor variations in floral structure occur. *L. gracilis*, sp. n., shows two of the corolla-lobes very slightly larger than the rest, and one of the five stamens is definitely shorter than the others, in these respects hinting at the lines along which the flower has evolved in Section II. TRICHOTOMI.

TEXT-FIG. 4.
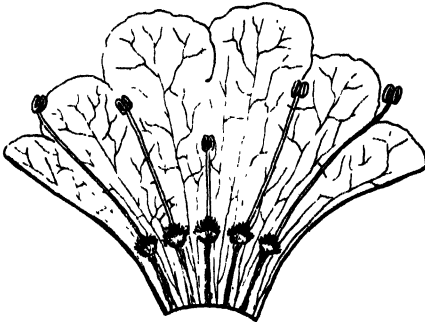
TEXT-FIG. 5.
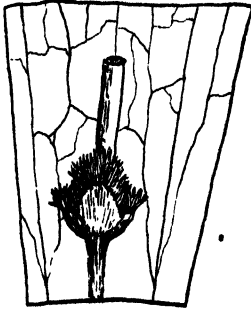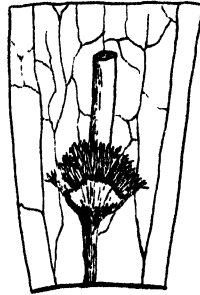
TEXT-FIG. 6.

TEXT-FIG. 7.

Fig. 4.—*Lobostemon glaucophyllus.* Corolla opened out, showing scales.   × 2.
Fig. 5.—*Lobostemon glaucophyllus.* Front view of scale.   × 6.
Fig. 6.—*Lobostemon hispidus.* Front view of scale.   × 6.
Fig. 7.—*Lobostemon glaucophyllus.* Longitudinal section through corolla, showing scale in section.   × 6.

Section II. TRICHOTOMI is linked on to Section I through *L. trichotomus* DC., a species which in some respects hovers between these sections, but the sum of whose characters places it in this section, and not in the previous one. The inflorescence is of the same type as in Section I, though each cyme does not elongate to such a marked extent. The flowers are larger, usually being more than 1 cm. in length. The corolla is of a different type from Section I, though occasionally in *L. trichotomus* forms appear which almost bridge the gap. The

typical corolla (seen split open in text-fig. 4) widens gradually from a narrow base. In the most highly organised species the corolla is definitely zygomorphic, this being due to an enlargement of two lobes. This is shown in *L. glauco-phyllus* (text-fig. 4) to a slight extent, but is very marked in *L. hispidus*. Except in some forms of *L. trichotomus* the corolla is glabrous outside. The scales are broader than in the previous section, and cup the base of the stamens. The dense upwardly directed hairs are here confined to the margin of the scale. Text-figs. 5 & 6 illustrate the range of differentiation exhibited by the staminal scales in this section. A comparison between text-figs. 7 and 3 will illustrate another difference between the scales of the two sections. Here the scale is directed upwards, not bending inwards as in Section I. The stamens in *L. tricho-tomus* are very nearly equal, but throughout the group a strong tendency is
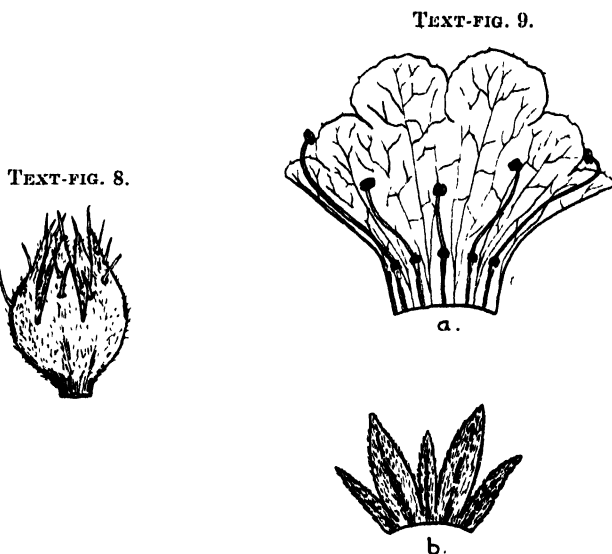
TEXT-FIG. 9.

TEXT-FIG. 8.

Fig. 8.—*Lobostemon stachydeus.* External view of calyx. × 2.
Fig. 9.—*Lobostemon argenteus.* a. Corolla opened out; internal view. b. Calyx opened out; external view. × 2.

exhibited to differentiation in size. Text-fig. 4 shows the highest aspect of staminal development in the section. It will be noted that one stamen (alter-nating with the two larger corolla-lobes in those species where differences exist in the size of the lobes) is much shorter than the rest. On either side of it come medium-sized stamens, while the remaining two are long. The long stamens are usually just exserted, but in *L. laevigatus*, and occasionally elsewhere, all the stamens may be exserted. Here, however, the whole aspect of the flower is very different from that in Section I. The stamens, especially the longer ones are usually adnate to the corolla for a *very short* distance above the insertion of the scales.

Section III. ARGENTEI contains only two species, and represents the end of an evolutionary line within the genus. The inflorescence marks it off sharply from all other sections. In *L. stachydeus*, which is the more primitive species, the inflorescence is a pseudo-spike, really consisting of a long bracteate axis with a cymule reduced to two flowers in the axil of each bract. Very rarely specimens may be found in which more than two flowers constitute the cymule, and in such the true cymose nature of each axillary branch is apparent. In *L. argenteus* the reduction is carried still further, as each lateral cymule is reduced to a single flower. The correctness of this interpretation is upheld by the fact that the main axis of the ' spike ' usually ends in a flower older than the flower lying immediately below it. The flowers are of medium size and zygomorphic.

The calyx is an important feature, as, taken with the inflorescence, it makes the identification of either of these species a simple matter. The calyx of *L. stachydeus* is shown in text-fig. 8. In most other species the calyx-segments are nearly free, while here they are joined for about a third of their length and the whole calyx is somewhat globose. In *L. argenteus* (text-fig. 9, *b*) two of the lateral segments are much larger than the rest. This is the most zygo- morphic species in the genus, as calyx, corolla, and stamens are all involved. In this group zygomorphism of the corolla is due to the enlargement of the two back lobes as in Section II, and the stamens are of the type described for the highest members of the same section (see text-fig. 9, *a*). One slight difference is that the four longer stamens are more distinctly adnate to the corolla above the insertion of the scales than in Section II. The corolla is nearly glabrous outside, but usually has scattered hairs along the central vein of each lobe and along the margins. The scales are much smaller than in either of the preceding groups, being small rounded structures or reduced to mere ridges (text-fig. 9, *a*).

Section IV. FRUTICOSI is the largest section of all, and contains some of the most showy members of the genus, the flowers rarely being less than 2 cm. in length. The inflorescence is of the same type as in Section II. The calyx is regular or in most species the front segment is rather shorter and narrower than the rest. The showy corolla widens gradually from a narrow base (text- fig. 10) and is somewhat zygomorphic, though in this section this feature is not as a rule due to the enlargement of two of the lobes, but to a general oblique trend of the whole corolla. The outer surface of the corolla is always hairy. The scales are reduced to mere hairy ridges (text-figs. 11 & 12), and above these the stamens are always adnate to the corolla-tube for some distance. The stamens are of three different lengths, as in the two previous sections (text-fig. 10).

Section V. GRANDIFLORA is a small group of three species, the evolutionary tendencies of which are quite different from those exhibited in the other groups. There the trend seems to be towards a greater degree of zygomorphism ; here,

while the corolla and stamens retain a primitive regularity, the calyx is asymmetrical and zygomorphism is not found in any of the three outer whorls.

The inflorescence is of the usual type similar to that of Sections II & IV. The flowers are large (*L. grandiflorus* has the largest flower amongst the Lobostemons). The calyx is unusually large and asymmetrical, least so in *L. montanus* (text-fig. 13, *b*), which in other respects as well comes close to

TEXT-FIG. 10.
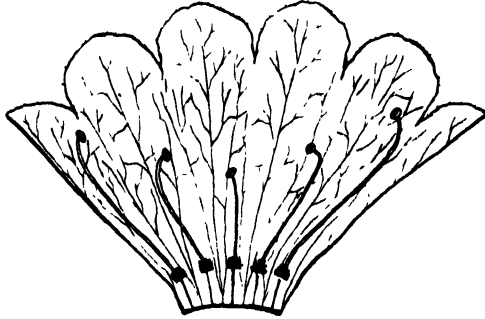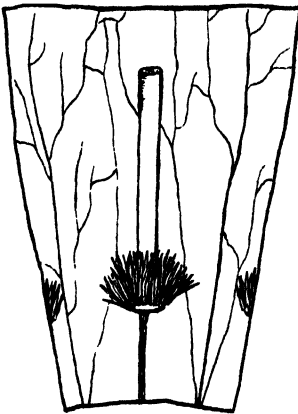
TEXT-FIG. 11.   TEXT-FIG. 12.
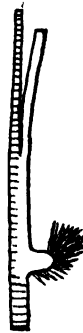
Fig. 10.—*Lobostemon fruticosus*. Corolla opened out ; internal view. × 2.
Fig. 11.—*Lobostemon fruticosus*. Front view of scale and base of one of longer stamens, adnate to corolla. × 6.
Fig. 12.—*Lobostemon Muirii*. Longitudinal section of corolla, showing the scale in section. × 6.

Section IV, and seems to indicate that it is an offshoot from it. In both the other species the calyx shows a high degree of asymmetry. In *L. sanguineus* the sepals are quite free, leaf-like, and of widely differing sizes (text-fig. 14). A modification of the asymmetrical calyx is seen in *L. grandiflorus*, where the unequal segments are joined in an irregular fashion, two of the segments usually

being joined for the greater part of their length. The corolla is hairy outside and tubular, sometimes attaining a length of 5 cm. in *L. grandiflorus* (text-figs. 13, *a*, & 15). In the other sections a bright blue is the predominating

TEXT-FIG. 13.

a.

b.
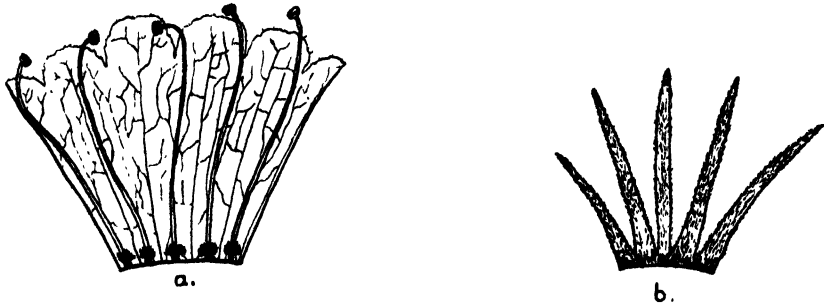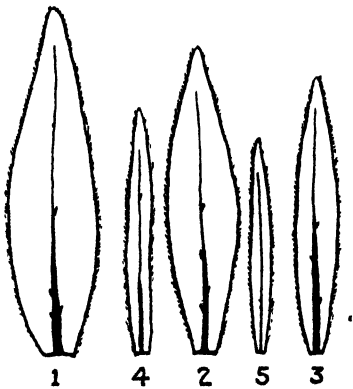
TEXT-FIG. 14.   TEXT-FIG. 15.

TEXT-FIG. 16.

1   4   2   5   3

c ——   —— f

—— s
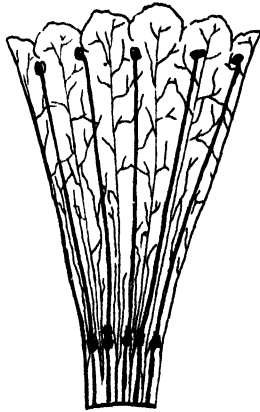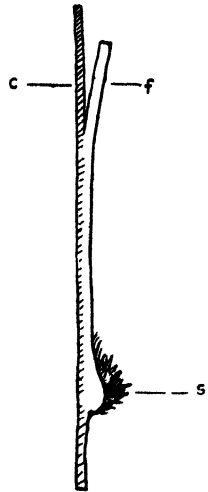
Fig. 13.—*Lobostemon montanus.*   *a.* Corolla opened out; internal view.   *b.* Calyx opened out; external view.   × 2.

Fig. 14.—*Lobostemon sanguineus.*   Sepals arranged in order.   × 2.

Fig. 15.—*Lobostemon grandiflorus.*   Corolla opened up down the front; internal view. Nat. size.

Fig. 16.—*Lobostemon grandiflorus.*   Longitudinal section through the corolla, showing the reduced scale.   *c* = corolla; *f* = filament; *s* = hairy swelling.   × 1½.

colour of the corolla, while here that colour has never been recorded. *L. montanus* is a pale faded blue, and the other two a brilliant red. The scales are much reduced. In *L. montanus*, where they are best developed, they are inserted almost at the base of the corolla (text-fig. 13, *a*), a lower position

than in any other species. In *L. grandiflorus* the scale is reduced to a mere hairy lump (text-fig. 16), this condition representing the greatest degree of reduction in the genus. The stamens are more or less equal in length, usually included, but sometimes exserted, in *L. montanus*. The filaments are adnate to the corolla for a considerable distance above the insertion of the scales.

It is obvious from the foregoing account that the flower of *Lobostemon* provides good diagnostic features on which to base a satisfactory subdivision of the genus. The untrustworthy vegetative features, which have been given undue prominence hitherto, should be relegated to a subordinate position.

The recognition of the five main sections is a comparatively simple matter, and herbarium material proved satisfactory in this connection. The chief difficulty, however, has been in trying to obtain a proper understanding of the limits of the species. At the time this research was started fifty-eight species were recognised, and my own early impressions based largely on herbarium specimens led me to believe that this was probably a low estimate. Since that time, however, careful studies in the field have forced me to the conclusion that many of the species are highly variable and that hybridisation undoubtedly occurs.

As in all South African taxonomic studies, problems of nomenclature soon became apparent. Some names had obviously been applied wrongly, and in order to clear up the confusion a visit to Europe was imperative. As I have now seen all important type-specimens, I am able to apply the names given in this paper with confidence. Full details of the many changes in nomenclature that have proved necessary are given under the various species (pp. 416–450).

At the outset in studying a problem of this nature we are faced with the old problem of what constitutes a species.

Lobostemon, like *Rubus*, *Rosa*, etc., is a genus which shows a bewildering number of forms, and before deciding what constitutes the Linnean species it is necessary in each to study the problem from as many angles as possible. Cytology has given some interesting results, but the publication of details on this aspect of the research is being withheld till further information is available. At this juncture it is sufficient to state that polyploidy is characteristic of the genus, seven being the basic number of chromosomes.

Evidence obtained from geographical distribution gives strong support to the present definition and grouping of the species, but a full discussion of the problems of distribution is being postponed till further information about certain species is available. Only those aspects essential to the argument are presented here.

Unfortunately, all breeding experiments have failed because it has not been possible to germinate the seed. This failure is probably due to the necessity for a long period of after-ripening, such as many South African plants require (14). This is suggested by the fact that some seeds of other genera, which were sown in one year and gave no results at the time, germinated during the rainy season a year later.

THE SPECIES PROBLEM IN LOBOSTEMON

In the summary of Sir Daniel Hall's address, given as an opening to the discussion on the species concept at the Fifth International Botanical Congress at Cambridge (5), he makes the following statement :—' A species is a category existing only in our own minds for purposes of classification, not an absolute entity, but a convenience.' How true this remark is, can be appreciated only by those who have attempted to place the boundaries between species in such a variable genus as *Lobostemon*. In *Passerina*, Professor Thoday (20) found that once the facts of structure and distribution were in his possession the species could easily be defined, and appeared to show little variation beyond such simple cases as differences in the colour of the perianth and so on. In *Lobostemon* this is very far from being so. It has been stated elsewhere in this paper that on herbarium evidence alone one would be tempted to create large numbers of species. Investigation carried out on living plants in their natural habitats, however, has shown that recognition of such micro-species only leads to obscuring the true state of affairs.

The first step in a problem of this nature is to determine how far each species is susceptible to changes in environment. Careful records of changes in habit, leaf-size, hairiness of the parts, and so on, under different environmental conditions, is an essential preliminary to a study of variation in general.

Usually differences produced by the environment were not found to be pronounced. In general, shade-forms have a more lax habit, fewer and softer hairs, and slightly larger leaves. Where species possess rather stiff bristles among the finer hairs, e.g. *L. argenteus*, these tend to stand out from the surface and show a more vigorous development in dry situations. Incidentally these bristles show a similar change during a single vegetative season. For example, in *L. argenteus*, grown in a relatively sheltered situation, during the spring and early summer when the shoots are young the bristles are obscure. As the season advances the bristles become stiffer and show the features of those found throughout the whole season in plants in dry situations. Failure to recognise this type of variability due to changes in environment and to seasonal differences led to the recognition of *L. argenteus* and *L. ferocissimus* as separate species. Field-studies of the two have shown that *L. ferocissimus* is merely a form of *L. argenteus* in which all the hairs stand away from the leaf instead of being adpressed and in which the bristles are strongly developed.

The inflorescence is another structure which shows a pronounced seasonal alteration. This is particularly marked in Section I. *Echioides*, and details have been given under that section of such changes occurring in *L. paniculatus*. *L. paniculatus* itself, not having a very wide distribution and not having been collected often, has escaped the fate of *L. echioides*, which, owing to its wide distribution and abundance in the areas in which it occurs, has suffered badly at the hands of taxonomists. *L. echioides* shows exactly the same changes in its inflorescence as *L. paniculatus* (see p. 396 ; Pl. 29). *L. fastigiatus* Buek

is merely *L. echioides* in which the inflorescence is fully expanded, and consequently cannot be regarded as a separate species.

Another feature that has led to some confusion is the behaviour of the leaf after the main period of vegetative and floral activity has come to an end. The leaf usually has a second growing-period later in the season. Correlated with this is a change in indumentum, either the hairs becoming stiffer or falling off and leaving their hardened bases behind. In any case, owing to the increase in size of the leaf, the hairs become more scattered during this second growing-period. Most species show this ' secondary growth ' in some degree. It is specially well marked in *L. curvifolius*, *L. echioides*, and *L. trichotomus*.

L. montanus, practically confined to the Cape Peninsula, proved itself to be an exception to the general rule and to be most susceptible to changes in environment. In the southern end of the Cape Peninsula, where it is most abundant, the plants usually grow in exposed situations on sandy soil. Here the leaves have an average size of 4 cm. in length and 1 cm. in width, and are silvery with densely packed, adpressed hairs. If the species be followed northward, we find a gradual tendency to restrict its distribution to the sheltered sides of shallow ravines. North of Constantia Nek it is never found anywhere but in sheltered places. As the plants adopt the more sheltered habitat we find a gradual change in leaf-size and hairiness.

On the eastern slopes of Devil's Peak, under extremely mesophytic conditions, plants grow with leaves measuring as much as 20 cm. in length and 5 cm. in width. The hairs then are widely spaced and are not adpressed, so at first sight the leaf looks extremely different from that of the southern form. Had the species not been traced from one end of the Peninsula to the other, and the gradual change in leaf-form in response to gradual change in habitat been noted, there is no doubt that two species (or a species and its variety) would have been described. Variation in floral structure bears no relation to the environment. The only floral variation that has been noted in this species is a form in which the stamens are exserted. This form occurs anywhere within the range of the species and appears to be a mutant, having no connection whatever with environmental conditions.

Before returning to the problem of mutation as distinct from seasonal and environmentally induced changes, a few general features should be noted. After a veld fire all species appear to possess the power of rapid regeneration from underground parts. The shoots that arise immediately after burning are much more vigorous than usual and have larger leaves, frequently twice as large as the normal type. When the leaves are hairy the hairs become more widely spaced, as in the habitat types of *L. montanus*. The same thing applies, though in a less degree, to plants that have been heavily grazed. In the field this phenomenon offers no difficulty in interpretation, but in herbarium specimens such marked differences in leaf-size have frequently led to erroneous determinations. When it is borne in mind that in the ' Flora Capensis ' leaf-size and hairiness are used as primary characters in the subdivision of the

genus, it will be obvious that the classification is based on variable, and there-
fore unreliable, characters.

Another factor of undoubted importance is hybridisation. *Lobostemon
glaucophyllus* may be taken as a good example. It is the most widespread
species in section *Trichotomi*, ranging from the Cape Peninsula to Namaqualand.
It is seldom found at altitudes above 3,000 feet. In the Piquetberg, Clanwilliam,
and Ceres districts *L. laevigatus*, a closely related species, is found at high alti-
tudes, usually about 4,000 feet. In the Zwart Ruggens, a small mountain
range lying some distance to the north of Ceres, *L. laevigatus* occurs without
L. glaucophyllus, and in that locality the purity of the species is undoubted.
In this isolated region its erect, sparsely branched habit, its relatively wide
spino-ciliate leaves, and its small, almost regular flowers mark it off sharply
from *L. glaucophyllus*. Its habitat, too, is distinctive, as it is confined to sheltered
places among rocks or in ravines. In the Clanwilliam district at altitudes of
4,000 feet and over it has the typical characters of the species, but below
4,000 feet, where it meets *L. glaucophyllus*, intermediate forms abound, and the
plants are no longer confined to sheltered places. A bewildering variety of
types leads to the conclusion that here we are dealing with what Allan, in New
Zealand, has termed a 'hybrid swarm' (I). Unfortunately, no breeding
experiments have been possible as yet, but there can be little doubt that
hybridisation has been responsible for the multiplicity of forms in these
districts.

L. Pearsonii is a common species on the lower mountain slopes round the
margin of the karoo. In the northern part of its area it frequently approaches
L. glaucophyllus and *L. laevigatus*, and it is probable that here, too, hybridisation
is playing an important rôle. However, the information from these northern
localities is very scanty, and until more information is available the question
must be left open.

A similar explanation may serve to elucidate some of the causes of variability
in *L. trichotomus*. In the part of the area occupied by it lying to the north
and west of Clanwilliam, several forms occur which are intermediate between
this species and the more glabrous species of the same section (*L. glaucophyllus*,
L. laevigatus, and *L. Pearsonii*). The areas of all four species coincide here,
and the supposition that *L. trichotomus* hybridises freely with any of them is
strong. For instance, at Zeekoe Vlei, near Clanwilliam, I have collected true
L. trichotomus and true *L. glaucophyllus*. I have also collected intermediate
forms, and other collectors have done the same. Schlechter, 8189, from
this locality is one of these intermediates, but has been determined as
L. cinereus DC. The type of *L. cinereus* was collected by Drège between
Heerenlogement and Kanagasberg. I have seen Drège's specimens in Berlin,
Paris, and Kew. Most of the Kew specimens approach *L. glaucophyllus* rather
closely, while the majority of the Berlin specimens come much closer to *L. tricho-
tomus*. One of the sheets in Berlin (labelled 'ex Herbar. E. Meyer') shows
a mixture of both forms. In view of all these facts, *L. cinereus* cannot be

considered a good species, and hybridisation is the most probable explanation of these intermediate forms. There is some evidence that *L. trichotomus* may hybridise with *L.laevigatus* and *L. Pearsonii*, but it is not so clear as in *L. glaucophyllus*.

In the neighbourhood of Wynberg and Kirstenbosch, on the Cape Peninsula, *L. trichotomus* shows another series of forms intermediate between it and *L. glaucophyllus*. Here the intermediates are rather different in appearance from those in the Clanwilliam area, but as the form of *L. trichotomus* which occurs on the Cape Peninsula is one of the mutant forms of the species (see p. 409) the different appearance of the presumed hybrids is to be expected. A single plant collected by Ecklon and Zeyher near Tulbagh, and the type of *L. acutissimus* Buek, is intermediate between *L. trichotomus* and *L. glaucophyllus*. As both species occur in the locality, the supposition that this plant is a hybrid receives considerable support. For this reason I have not retained *L. acutissimus* as a species, but have placed it among the presumed hybrids of *L. trichotomus*.

L. strigosus and *L. trigonus* appear to parallel the case of *L. glaucophyllus* and *L. laevigatus*. In the east, *L. trigonus* is an easily recognised species, and the same applies to *L. strigosus* in the west. In the neighbourhood of Mossel Bay, where their areas overlap, intermediate forms appear to be common. Here, however, I have no field-knowledge of the species, and will therefore do no more than suggest that the Mossel Bay forms may constitute a ' hybrid swarm '.

The only other clear case of hybridisation is Zeyher, 4842, from Camps Bay. This is intermediate between *L. fruticosus* and *L. argenteus*, both as regards floral structure and the inflorescence. Both these species occur together in this locality, but as their flowering seasons only just overlap the chances of hybridisation are minimised.

Once a clear understanding has been obtained of the extent to which the different species are susceptible to environmental and seasonal changes, and to hybridisation, the way is clear to a study of true mutation. Undoubtedly the best way in which to study this phenomenon is by means of breeding experiments in which environmental conditions are controlled, but the results given here have had of necessity to be based on field-observations and comparison of a very large number of herbarium specimens.

For convenience, a simple case will be taken first—that of *L. hispidus*. Every now and then, throughout the range of the species, odd plants occur not quite as tall as the type, with much smaller and more closely packed leaves and with divaricate branching quite distinct from the stiffly erect branching of the type. The inflorescence is affected by the general crowding of the organs, but the flowers are unaltered. As might be expected, the hairs on the leaves are more crowded in the small-leafed mutant form than in the type. This mutant form, which incidentally is Thunberg's type of *L. hispidus*, has been collected wherever the normal form occurs. It is never common, always occurring

as an odd plant here and there growing with normal plants. The inference seems clear. The small-leafed form is not a separate species, but a mutant, which is constantly being produced by normal plants. Similar mutants are known to occur in other plants where pedigrees are known. For instance, among Oenotheras the dwarf forms which frequently appear in pedigree cultures are of the same type as these mutant plants of *L. hispidus*. Miss Gairdner (10) quotes and figures a similar case in *Campanula persicifolia*, where a dwarf form ' nitida ' has occasionally turned up as a mutant among pedigree plants. These ' nitida ' plants show exactly the same type of reduction in leaf-size and crowding of the leaves as the small-leafed form of *L. hispidus*.

A second mutant type occurs among plants of *L. hispidus*—a giant form. Gigantism in this species is never very pronounced, and is easily overlooked, but once these larger forms are recognised it is seen that they are strictly comparable in their occurrence and frequency with the small-leafed form. ' Giant ' mutants are probably amongst the most common mutations among plants.

The only other type of variation which, up to the present, has been recognised in *L. hispidus* is that of flower-colour. White is the normal colour, but blue-flowered plants frequently turn up.

The small-leafed mutant form is of special interest in *Lobostemon* because it appears to be one to which the genus as a whole is particularly prone. It occurs frequently in the following species :—*L. echioides* (see Pl. **29**), *L. capitatus*, *L. Bolusii*, *L. trichotomus*, *L. Pearsonii*, *L. glaucophyllus*, *L. fruticosus*, and *L. curvifolius*. Three species have been created in the past for mutants of this type : viz. *L. microphyllus* Buek in *L. echioides*, *L. capitiformis* DC. in *L. capitatus*, and *L. magnisepalum* N. E. Br. in *L. curvifolius*.

The giant form had been recognised in several species, other than *L. hispidus*, viz. *L. echioides*, *L. trichotomus*, *L. Pearsonii*, and *L. laevigatus*, though none has been described as a distinct species, probably because they have been regarded as luxuriant forms due to environment. This is not so, however, as the giant forms occur with the normal, and show no differences of habitat.

Another feature which shows great mutability is the type of hairiness. *L. echioides* may be taken as an example of this. In this species the leaves and stems are covered with hairs of two types—very fine ones which tend to be adpressed, and much coarser ones which frequently stand out from the surface. In the form of this species common from Robertson to Riversdale, the coarser outstanding hairs predominate and the leaves are rough to the touch and not silvery. North of the Langeberg the finer adpressed hairs are more abundant than the coarse, and the plants appear silvery. If these plants remained constant in their respective localities, there would be a good case for regarding them as two species ; but they do not. South of the Langeberg silvery mutants are met with occasionally, and north of the Langeberg the non-silvery form turns up equally often among the usual silvery forms. A comparison of a large number of specimens from various localities has led me to

reject attempts I made during the early stages of the work to establish separate species. Possibly, when we have more data, it may be possible to split the species, but at present it is best regarded as highly variable in its vegetative characters.

Several other species show exactly the same type of variability in indumentum. *L. trichotomus* in the Zwart Ruggens, north of Ceres, usually has silvery leaves, but occasionally mutant forms occur in which the hairs are shorter and scattered. The rough texture of the older leaves led this form to receive the name *L. verrucosus* Buek. Further south, in the neighbourhood of Tulbagh, both forms occur, but the ' verrucosus ' form is the common one. On the Cape Peninsula, where the species is rather local, the ' verrucosus ' form is the only one recorded up to the present. *L. argenteus* is another example of the same phenomenon. In the west the common form has adpressed hairs, and when the hairs are not too coarse it is silvery. Occasionally forms occur with hairs standing away from the surface. Such forms are common in the eastern part of its area of distribution (*L. pilicaulis* C. H. Wright is this form), while they occur only here and there in the west. *L. fruticosus*, *L. lucidus*, and *L. trigonus* afford still further examples of comparable variation in the types of indumentum which may be observed.

The mutational changes just described are of fundamental importance in the genus, but several others occur. In *L. trichotomus*, *L. Pearsonii*, and *L. fruticosus* plants with much smaller flowers than the type, but in all other respects similar, appear occasionally. *L. trichotomus* is the only species which shows definite variation with regard to the absence and presence of hairs on the outer surface of the corolla. In all other species this character appears to be constant.

Flower-colour is subject to variation. In those species which have blue flowers, pink-flowered plants commonly occur. This phenomenon is marked in *L. fruticosus*, where in some localities plants with pink flowers are more common than those with blue. White-flowered forms, with all parts destitute of colouring-matter other than chlorophyll, have been observed in a few of the species. Here, again, *L. fruticosus* appears to be most susceptible to this variation. Occasionally forms with exserted stamens appear in species which normally have included stamens. This has been recorded for *L. montanus* and *L. glaucophyllus*.

The only species in *Echiostachys* showing a pronounced tendency to vary is *E. spicatus*, where the degree of hairiness of both leaves and peduncles ranges from almost glabrous to villous.

Two cases have been recorded, one in *Lobostemon*, and one in *Echiostachys*, where the mutant has lost one of the typical characters of the genus to which it belongs. The first is that of a single specimen of *L. Pearsonii*, found growing with normal plants at Tweedside, near Matjesfontein. Here the staminal hairs and scales were completely absent, though otherwise the plant showed no unusual features. The other was noted in a herbarium specimen of *Echiostachys spicatus*. This is one of the two specimens of Drège, 7854, at Kew

The anthers, instead of being short and rounded as they are in both *Echiostachys* and *Lobostemon*, are rather long and distinctly versatile. It is of considerable interest to find that in both these genera even the generic characters are liable to fluctuation in rare instances.

In summing up the position it may be stated that variability in both genera is largely restricted to vegetative features, while floral characters are relatively stable. The reason for the confusion in the past with regard to *Lobostemon* is now obvious. Any system of classification emphasising vegetative features and neglecting floral structure could not prove satisfactory.

A fact that emerges with great clarity in this investigation is that the same type of mutation occurs again and again in different species of the genus. Vavilov (21) has termed this phenomenon 'the law of homologous series in variation', and has shown it to apply in numerous cultivated plants. The position may be summarised in Vavilov's own words :—

'1. Linneons and genera more or less nearly related to each other are characterized by similar series of variation with such a regularity that, knowing a succession of varieties in one genus and Linneon, one can forecast the existence of similar forms and even similar genotypical differences in other genera and Linneons. The similarity is the more complete as the Linneons and genera are more nearly allied.

'2. Whole botanical families in general are characterized by a definite cycle (series) of variability which goes similarly through all genera of the family.'

It has been shown that within several of the species (notably *L. echioides*, *L. trichotomus*, and *L. hispidus*, but among others as well) similar series of variation occur (see Table I, p. 449, for a summary). Recognition of this fact has led to a much clearer understanding of the species or Linneon in *Lobostemon*. Some of the species appear to be monotypic in nature, but this may well be because they are insufficiently known. Other species are highly polymorphic, and exhibit a definite series in variation. With increase of knowledge the series in each case will probably be much extended. To regard any one member of a series as a species (which has been done in the past) only makes for confusion. The conception of a species as a system of forms leads to a proper understanding of the genus as a whole.

Vavilov's law holds equally well in considering the sections of the genus. Here, too, a parallelism in evolution may be discerned. Taking those species with hairy vegetative parts as primitive, and the glabrous forms as derived, the parallel lines are indicated in Table II (p. 450). (Section III. has been omitted as · it contains only two species both of which are hairy in their vegetative parts.)

In *Lobostemon* polyploidy has been demonstrated, but the small size and almost uniform characters of the chromosomes have rendered impossible their morphological analysis. However, as it is known in other plants that mutants frequently have characteristic chromosome differences from the type, it is of special interest to note the conditions under which these chromosome changes occur,

Hagerup (11) has demonstrated that extremes of heat in the Sahara and cold in the Arctic zone lead to the production of polyploids in those regions, and he is of the opinion that polyploidy has played an important part in the production of new species suited to the difficult conditions of life in those parts. Several investigators, amongst them Sakamura and Stow and Heilborn, have shown that polyploidy can be induced under artificial conditions by extremes of temperature. Goodspeed and Michaelis have produced polyploids under the influence of X-rays, and Jørgensen (12) has shown that they are frequently produced in somatic tissues in *Solanum* as a result of wounding.

The work of Navashin (15) is of exceptional interest in that he was able by the use of X-rays to alter not the number but the configuration of the chromosomes in *Crepis tectorum*. He used soaked seeds which were exposed to X-rays for varying lengths of time. The seedlings which arose from seeds which had been exposed for a suitable length of time showed many abnormalities, and when a cytological examination was made it was found that, although the numbers remained the same, the shapes of the chromosomes were different. Navashin was able to demonstrate that these changes in configuration were due to dislocation and subsequent fusions of chromosome parts.

Thus there is definite evidence that nuclear changes may be induced in both gametic and somatic tissues by X-rays, wounding, and extremes of temperature. This has an important application in the case of *Lobostemon*. Over-grazing and veld-burning occur frequently in those parts of South Africa where Lobostemons grow. Again and again the aerial parts of plants are destroyed, but neither fire nor grazing is able to kill the subaerial parts of these plants. Buds situated at or just below the level of the soil immediately produce new shoots. There is no evidence to show that regeneration from seed plays an important rôle in the life of species of *Lobostemon*. In fact, seedlings are rarely seen. Conditions, however, are present for the production of mutations from somatic tissues. During a veld fire very high temperatures are experienced. In addition, after the vegetal covering has been removed, the heat of the sun has full effect on the buds lying near the surface of the soil. I have been able to show in some experiments that are still in progress that at Rondebosch, where the climate is mild compared with that of the south-western belt as a whole, temperatures of over 60° C. are experienced on a hot summer's day 2·5 cm. below the level of a sandy soil such as most Lobostemons favour. Along the borders of the karoo, a region where Lobostemons are unusually variable, the temperatures must be considerably higher. Heat is likely to be a factor inducing mutations under these circumstances. Cold is probably not of much importance at low altitudes, but at about 4,000 feet and over the tremendous daily range of temperature is a factor that cannot be neglected. Some years ago I was studying the vegetation of the Zwart Ruggens at an altitude of 4,000 feet. It was late September (the South African spring) and during the day the air was warm, but every night the temperature sank below 0° C. In the winter still lower temperatures must be experienced at

night.   In that locality *L. trichotomus,* which was not growing with any other species, was very variable.   Cold or the great daily range of temperature may be operative in inducing mutations in such localities.

Sheep and goats find certain species of *Lobostemon* most palatable, and eat every available shoot when the chance is offered.   Such species are *L. echioides* and *L. trichotomus,* both, it will be noted, variable species.   The wound-reactions in such cases might well induce mutations such as Jørgensen (12) has shown to occur repeatedly in *Solanum* as a result of wounding.

It is significant that the region in which greatest variability in *Lobostemon* has been seen is on the borders of the karoo.   Here conditions only just permit the existence of the south-western vegetation, and an extremely small change in the environment may cause an entirely different type of vegetation to become dominant.   Under these conditions mutant forms comprise a large proportion of the total population.

Lobostemon is a genus where, though some of the species seem to have reached a point of stable equilibrium, many have not, and under conditions favouring mutation show a ready response.
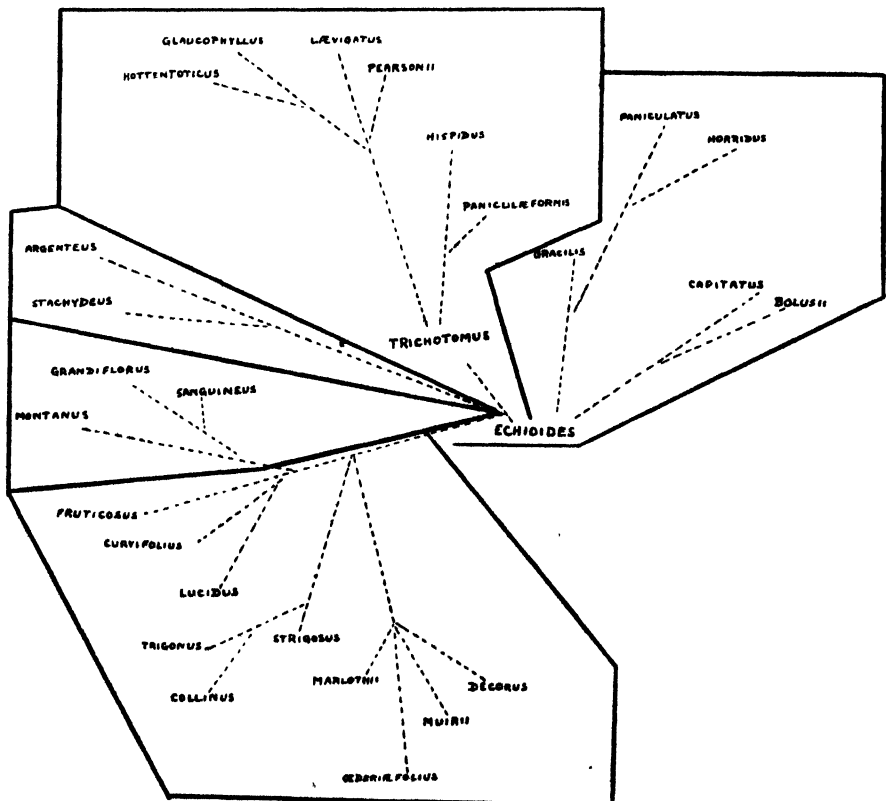
Diagram to illustrate the inter-relations of the species of *Lobostemon.*

LOBOSTEMON Lehm. in Linnaea, v (1830), p. 378.

Flowers bisexual, 5-merous. *Sepals* free or nearly so, rarely joined for part of their length, similar or dissimilar. *Corolla* tubular or funnel-shaped ; regular or zygomorphic ; lobes equal or two larger than the rest, erect or spreading ; provided with a densely hairy scale, ridge, or protuberance at the base of the stamens. *Stamens* 5, epipetalous, exserted or included ; filaments well developed, equal or unequal, glabrous ; anthers subglobose, obtuse. *Ovary* superior, 4-lobed with a gynobasic style, on a flat or slightly convex disc. *Style* simple, with a minutely bilobed stigma, glabrous or hairy. *Nutlets* 4, distinct, erect, ovoid-trigonous or acuminate ; tuberculate or rugose-tuberculate, rarely almost smooth ; occasionally with tufts of glass-like spicules on the tubercles ; attached by a flat base. *Seeds* straight.

Shrubs or undershrubs, rarely almost herbaceous ; scabro-canescent or hairy, rarely almost glabrous. Leaves alternate, sessile, hairy, or nearly glabrous ; sometimes armed with spiny hairs. Inflorescence of few or many scorpioid cymes ; rarely reduced to a pseudo-spike ; bracts usually conspicuous ; cymes more or less elongated in fruit. Flowers commonly blue, but red, pink, white, and greenish yellow coloured flowers occur.

An endemic South African genus. Species 28.

Key to the Sections.

A. Inflorescence a pseudo-spike, with one or two flowers in the
   axil of each bract.................................. Sect. III. ARGENTEI.
AA. Inflorescence of several well-developed cymes.
   B. Corolla with a narrow tube at the base, widening
      abruptly ; the lobes spreading more or less horizontally. Sect. I. ECHIOIDES.
   BB. Corolla widening gradually from the base ; the lobes not
      as above.
      C. Corolla tubular; stamens equal or nearly equal in length. Sect. V. GRANDIFLORI.
      CC. Corolla funnel-shaped; stamens usually of three lengths.
         D. Corolla glabrous outside (exc. some forms of *L. tri-
            chotomus*) ; staminal scales usually well-developed.. Sect. II. TRICHOTOMI.
         DD. Corolla usually hairy outside; staminal scales
            reduced to mere ridges .... Sect. IV. FRUTICOSI.

Key to the Species.

Section I. ECHIOIDES. *Inflorescence* of several to many cymes which usually elongate greatly in the fruiting stage. *Sepals* equal or nearly equal ; much shorter than the corolla. *Corolla* regular or with two lobes larger than the rest ; having a narrow cylindrical basal portion, above which it expands abruptly and widely ; glabrous or hairy outside. *Staminal scales* well developed, sharply or bluntly triangular, with two lateral lobes. *Stamens* equal or subequal, or with one shorter than the rest, far exserted from the corolla, free or hardly adnate above the insertion of the scales. *Style* glabrous or nearly so. *Nutlets* rather pointed.

A. Corolla 6 mm. in length or less ; flowers never a true blue.
   B'. Leaves linear or lanceolate ; flowers often with brown and
      purplish markings .... 5. *capitatus.*
   B'B'. Leaves ovate or ovate-lanceolate ; flowers white .... 6. *Bolusii.*

AA. Corolla more than 6 mm. in length; flowers usually a
 true blue.
  B². Leaves a true green, minutely strigose or with pungent
   bristles.
   C. Leaves minutely strigose; two corolla-lobes definitely
    larger than the rest .... 4. *gracilis.*
   CC. Leaves with scattered pungent bristles; corolla regular
    or with two lobes very slightly larger than the rest.
    D. Leaves lanceolate to ovate-lanceolate; with the
     thickened margin and projecting midrib on the lower
     surface armed with spine-like bristles .... 3. *horridus.*
    DD. Leaves linear; midrib on the lower surface and the
     margin bristly, but not spiny..................... 2. *paniculatus.*
  B²B². Leaves not a bright green; covered with numerous hairs
   which are not pungent .... 1. *echioides.*

Section II. TRICHOTOMI. *Inflorescence* of several cymes which elongate moderately in
the fruiting stage. *Sepals* equal or nearly so, half as long as the corolla or less. *Corolla*
with a strong zygomorphic tendency, leading to its highest development in *L. hispidus,*
where the two posterior lobes are much larger than the rest; corolla rarely quite regular,
funnel-shaped, glabrous outside (exc. some forms of *L. trichotomus*). *Staminal scales*
usually well developed, triangular or rounded, often with two lateral lobes; main portion
of the scale may be somewhat acute, but is never very sharply pointed. *Nutlets* somewhat
pointed.

 A. Young stem glabrous or nearly so; under surface of the leaf
  glabrous, or if with some hairs then the hairs are not uni-
  formly distributed.
  B'. Plants sparsely branched, with a stiff, erect habit; leaves
   usually spiny along the margin; staminal scales some-
   what pointed....................................... 10. *laevigatus.*
  B'B'. Plants somewhat divaricately branched; leaves with or
   without spines on the margins; staminal scales rounded
   at the apex.
   C'. Bracts nearly always spiny; flowers usually whitish.... 12. *hottentoticus.*
   C'C'. Bracts rarely spiny; flowers usually blue, sometimes
    pink, very rarely white.
    D. Average length of leaf 25 mm., if larger then more
     than five times as long as broad .... 13. *Pearsonii.*
    DD. Average length of leaf considerably more than 25 mm.;
     usually less than five times as long as broad.......... 11. *glaucophyllus.*
 AA. Young stem distinctly hairy; leaves hairy at any rate on the
  lower surface.
  B². Upper surface of leaf glabrous or nearly so .... 9. *paniculaeformis.*
  B²B². Upper surface of leaf distinctly hairy.
   C². Two posterior corolla-lobes much larger than the rest;
    corolla usually white; hairs on the leaf bristly, standing
    out from the surface .... 8. *hispidus.*
   C²C². Two posterior corolla-lobes slightly larger than the rest
    or all the lobes equal; corolla usually blue or pink;
    hairs on the leaf adpressed; leaf often silvery .... 7. *trichotomus.*

Section III. ARGENTEI. *Inflorescence* a pseudo-spike, with one or two flowers in the axils of the bracts. *Sepals* equal or unequal. *Corolla* zygomorphic, the two posterior lobes larger than the rest, funnel-shaped, glabrous outside or with a few hairs along the central vein of each lobe and along the margin. *Staminal scales* small, rounded, or reduced to a mere ridge. *Stamens* of three distinct lengths. *Style* hairy.

A. Calyx regular or nearly so ; staminal scales minute ; normally two flowers in the axil of each bract .... 14. *stachydeus.*

AA. Calyx with the two lateral sepals larger than the rest ; scales small and rounded ; normally only one flower in the axil of each bract .... 15. *argenteus.*

Section IV. FRUTICOSI. *Inflorescence* of several well-developed cymes, which elongate moderately in the fruiting stage. *Sepals* equal or slightly unequal in size ; in the latter case one is smaller than the rest. *Corolla* somewhat zygomorphic, due to a general obliquity of the whole, rarely with two lobes larger than the rest, funnel-shaped, usually hairy on the outer surface. *Staminal scales* small, reduced to mere transverse ridges. *Stamens* of three lengths, rarely with the four longer stamens approximately equal ; the longer stamens always adnate to the corolla for some distance above the insertion of the scales ; never far exserted. *Style* hairy.

A. Leaves glabrous or nearly so.

    B'. Leaves oblong, obtuse ; usually less than 3·5 cm. .... 21. *collinus.*

    B'B'. Leaves linear, acute, usually more than 3·5 cm.

        C'. Leaves pale green ; calyx about as long as the corolla-tube ; corolla greenish cream with red veins.......... 23. *Muirii.*

        C'C'. Leaves deep green ; calyx shorter than the corolla-tube ; corolla usually a bright blue .... 24. *decorus.*

AA. Leaves hairy or bristly when young.

    B^2. Calyx glabrous except along the margin and central vein of each lanceolate sepal .... 22. *oederiaefolius.*

    B^2B^2. Calyx hairy or bristly.

        C^2. Habit not shrubby ; woody portion of the stem not coming much above ground-level ; inflorescence of several loose cymes .... 18. *lucidus.*

        C^2C^2. Habit shrubby ; with definite branching ; inflorescence of compact or regularly arranged unilateral cymes.

            D. Young leaves densely covered with rather silvery adpressed hairs.

                E'. Leaves oblanceolate or obovate, rarely linear ; usually not closely imbricate ; apex of the leaf not recurved. 16. *fruticosus.*

                E'E'. Leaves linear or linear-lanceolate, usually imbricate and recurved at the apex .... 17. *curvifolius.*

            DD. Young leaves strigose or bristly.

                E^2. Leaves covered with numerous closely adpressed hairs, never very obtuse.

                    F'. Hairs on calyx rather soft .... 16. *fruticosus.*

                    F'F'. Hairs on calyx bristly .... 25. *Marlothii.*

                E^2E^2. Leaves bristly, with hairs standing out from the surface, if hairs adpressed, then apex very obtuse.

                    F^2. Leaves oblong, blunt ; average length 2 cm. ; cymes rather congested when young .... 20. *trigonus.*

                    F^2F^2. Leaves linear or linear-oblong ; average length more than 2 cm. ; bristles harsh ; cymes spreading when young ....·.............. 19. *strigosus.*

Section V. GRANDIFLORI. *Inflorescence* of a number of crowded cymes. *Calyx* sub-regular to asymmetrical. *Corolla* regular, tubular; hairy outside, at any rate in the upper portion. *Staminal scales* much reduced, mere hairy lumps or ridges. *Stamens* equal in length or nearly so. *Style* hairy. *Nutlets* (where these are known) almost smooth in the upper part, faintly tuberculate below.

A. Leaves hairy; sepals not very dissimilar; scales almost at the
    base of the corolla-tube; flowers pale blue................ 26. *montanus.*
AA. Leaves, apart from stiff spine-like hairs on the margin and the
    midrib, glabrous, at any rate on one surface; sepals dis-
    similar; scales not at the base of the tube; flowers red.
    B. Leaves glabrous below; at least two of the sepals joined;
       corolla-tube 4 to 5 cm. long .... 27. *grandiflorus.*
    BB. Leaves glabrous above; sepals all free; corolla-tube 3 cm.
       long or less .... 28. *sanguineus.*

1. LOBOSTEMON ECHIOIDES Lehm. in Linnaea, v, p. 378, tab. 5, fig. 1 (1830); DC. Prod. x, p. 9 (1846); C. H. Wright in Fl. Cap. iv, 2, p. 37 (1904). *L. Lehmannianus* Buek in Linnaea, xi, p. 141 (1837). *L. elongatus* Buek in Linnaea, xi, p. 140; DC. Prod. x, p. 8; C. H. Wright in Fl. Cap. iv, 2, p. 35. *L. diversi-folius* Buek in Linnaea, xi, p. 140; DC. Prod. x, p. 9; C. H. Wright in Fl. Cap. iv, 2, p. 36. *L. fastigiatus* Buek in Linnaea, xi, p. 141; DC. Prod. x, p. 9; C. H. Wright in Fl. Cap. iv, 2, p. 37. *L. virgatus* Buek in Linnaea, xi, p. 142; DC. Prod. x, p. 11; C. H. Wright in Fl. Cap. iv, 2, p. 43. *L. microphyllus* Buek in Linnaea xi, p. 142; DC. Prod. x, p. 12; C. H. Wright in Fl. Cap. iv, 2, p. 36. *L. nitidus* Bolus; C. H. Wright in Fl. Cap. iv, 2, p. 38. *L. pubiflorus* C. H. Wright in Fl. Cap. iv, 2, p. 39. *Echium echioides* 1. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924). *E. diversifolium* I. M. Johnston, *l. c.* *E. fastigiatum* I. M. Johnston, *l. c.* *E. Buekii* I. M. Johnston, *l. c.* p. 51. *E. virgatum* I. M. Johnston, *l. c.* p. 52. *E. microphyllum* I. M. Johnston, *l. c.* *E. nitidum* I. M. Johnston, *l. c.* *E. pubiflorum* I. M. Johnston, *l. c.*

A shrub with erect or divaricate branches; up to about 80 cm. in height. *Branches* covered with a mixture of fine and coarse hairs which may be adpressed or not. *Leaves* extremely variable in size and indumentum; either spreading or imbricate, linear, linear-lanceolate, or ovate, acute or obtuse, ranging from 1 to 6 cm. in length and 3 to 6 mm. in width; both surfaces hairy, though the upper usually less so, and occasionally nearly glabrous; hairs of two kinds, fine and coarse; in forms where the coarse hairs predominate these usually stand out from the surface and the leaf is coarsely hispid; in forms where the fine hairs predominate these may be adpressed and give the surface a silvery . appearance; in old leaves the fine hairs may fall off. *Inflorescence* cymose, branches congested when young, but spreading greatly in the fruiting stage. *Bracts* similar to the leaves, but much smaller and ovate. *Calyx* about as long as the cylindrical portion of the corolla-tube or a little longer; sepals equal, linear or lanceolate, acute, covered outside with a mixture of fine and coarse hairs. *Corolla* with a narrow cylindrical tube, half the total length of the corolla or less, upper portion spreading outwards rather abruptly, regular,

usually less than 1 cm. in length ; lobes distinctly hairy outside ; usually blue. *Staminal* scales inserted at the entrance of the cylindrical portion of the tube, triangular with two lateral lobes, densely hairy, the hairs usually extending on to the corolla-tube as well, projecting almost horizontally and blocking the throat of the corolla. *Stamens* equal or subequal, much exserted, and free from the corolla above the insertion of the scales. *Style* glabrous. Each *nutlet* rather pointed with three longitudinal ridges ; rugose-tuberculate, the largest tubercles on the ridges.

Habitat. Usually a constituent of rhenosterveld.

Flowering season. Chiefly August to October, but frequently found at other times as well.

NAMAQUALAND : Spektakel, *Bolus* 642 ! Ezelsfontein, *Whitehead* ! between Brakdam and Rietkloof, *Pearson* 5663 ! Modderfonteinberg, *Drège* 7844 a ! *Scully* 171 ! *von Schlicht* 3454 ! VAN RHYNSDORP : Bitterfontein, name of collector not given ! CERES : near Ceres, *Levyns* 1050 ! Verkeerde Vlei, *Rehmann* 2836 ! between Hottentot's Kloof and Karoo Poort, *Pearson* 4812 ! Gydouw Pass, *Bolus* 8387 ! Karoo Poort, *Hutchinson* 432 ! TULBAGH : *Ecklon and Zeyher* ! CALEDON : Genadendal, *Schlechter* 10334 ! *Ecklon and Zeyher* ! *Drège* 3452 ! WORCESTER : Goudini Road, *Levyns* 1492 ! near de Doorns, *Bolus* 13158 ! Hex River, *Tyson* ! Tafelberg, *Rehmann* 2761 ! *Pillans* 14151 in Herb. Bolus ! Pietermeintjes, *Marloth* 9964 ! *Rogers* 16538 in Herb. Bolus ! Tweedside, *Compton* 3194 ! *Compton* 3197 ! *Levyns* 2363 ! *Levyns* 2366 ! *Levyns* 2771 ! Whitehill, *Compton* 3195 ! *Compton* 2074 ! ROBERTSON : Robertson, *Levyns,* 2773 ! Cogman's Kloof, *Kuntze* ! *Levyns* 129 ! Montagu, *Bolus* 8296 ! between Montagu and Barrydale, *Levyns* 417 ! Concordia, *Levyns* 276 ! *Levyns* 2574 ! SWELLENDAM : Swellendam, *Ecklon and Zeyher* ! *Zeyher* 3452 ! *Mundt* ! *Pappe* ! *Burchell* 7453 ! Barrydale, *Galpin* 4347 ! *Hutchinson* 1098 ! Tradouw Pass, *Marloth* 8614 ! Bonnievale, *Marloth* 11841 ! LADISMITH : Zandkraal, *Muir* 4487 ! Ladismith, *Levyns* 2096 ! *Levyns* 2722 ! RIVERSDALE : Zoet-melk's River, *Burchell* 6690 ! Vet River, *Burchell* 6848 ! Riversdale, *Muir,* 347 ! *Bolus* 11351 ! *Muir* 4540 ! *Muir* 4171 ! *Muir* 4539 ! *Muir* 4357 ! *Ecklon and Zeyher* ! *Rust* 84 ! *Schlechter* 1927 ! *Levyns* 2618 ! *Levyns* 2863 ! Corente River, *Muir* 5153 ! Oakdale, *Muir* 5260 ! *Levyns* 3505 ! *Levyns* 3511 ! MOSSEL BAY : between Little Brak River and Hartenbosch, *Burchell* 6204 ! *Burchell* 6224 ! foot of the Langeberg, *Muir* 1390 ! PRINCE ALBERT : north of Seven Weeks' Poort, *Levyns* 2335 ! north of the Zwartberg, *Muir* 4358 ! Zwartberg Pass, *Bolus* 11635 ! GEORGE : Kamanassie hills, *Alexander* ! Great Brak River, *Schlechter* 5757 ! UNIONDALE : Kamanassie, *Bolus* 2436 ! Langkloof near Haarlem, *Fourcade* 1330 ! Langkloof, *Ecklon and Zeyher* ! GRAAFF REINET : *Bolus* 698 ! UITENHAGE : van Stadensberg, *Drège* ! SOMERSET EAST : *Bowker* ! BATHURST : Port Alfred, *Rogers* 17172 ! No LOCALITY : *Alexander, Ecklon and Zeyher* (partly) ! *Zeyher* 232 ! *Oldenburg* ! *Bowie* !

Note.—This is an extremely polymorphic species. I have based the species on Lehmann's description, though it has been necessary to modify it. Plants

with the leaves glabrous on the upper surface do occur (especially plants grown in shade), though the leaves normally have hairs on both surfaces. Lehmann's plant was grown in the Botanic Gardens at Hamburg, and it seems likely that the leaf-characters he describes were largely due to conditions under which the plant was growing. With regard to floral characters his descriptions agree perfectly with the species as defined here.

2. LOBOSTEMON PANICULATUS Buek in Linnaea, xi, p. 139; DC. Prod. x, p. 8; C. H. Wright in Fl. Cap. iv, 2, p. 33. *Echium paniculatum* Thunb. Prod. Pl. Cap. p. 33 (1794); Willd. Sp. Pl. t. i, 2, p. 784 (1798); Pers. Syn. Pl. i, p. 163 (1805); Thunb. in Schrad. n. Journ. i, 3, p. 41 (1806); Lehm. Pl. Asper. p. 425 (1818); Lehm. Ic. t. xxiii (1821), not of Drège; Thunb. Fl. Cap. ed. Schult. p. 165 (1823).

An undershrub, when growing in the shade almost herbaceous, but always with a woody base, reaching about 60 cm. in height, moderately branched. *Branches* setose, with coarse and fine bristles mixed, the coarse bristles becoming more apparent with age. *Leaves* linear, obtuse or somewhat acute, with a prominent midrib on the lower surface, very variable in size, ranging from 2 to 8 cm. in length, and from 3 to 8 mm. in width, under surface and margin beset with stiff, scattered, bulbous-based bristles, with a few smaller bristles interspersed; upper surface with rudimentary bristles, sometimes appearing glabrous when young; both surfaces becoming much more bristly with age. *Inflorescence* cymose, cymes much contracted when young, but elongating greatly in the fruiting stage. *Bracts* not larger than the flowers, similar to the leaves in texture and bristliness, but much smaller, varying in shape from lanceolate to ovate. *Calyx* about as long as or a little longer than the cylindrical portion of the corolla-tube; sepals equal, linear-oblong, usually obtuse, beset with stiff, upwardly directed bristles, both coarse and fine. *Corolla* with a narrow cylindrical basal portion, about one-third of the total length, upper portion spreading outwards rather abruptly, regular, with somewhat oblong lobes; under 1 cm. in length; almost glabrous except for a few bristles along the centre veins; the lobes occasionally ciliate; colour usually blue. *Staminal scales* inserted at the entrance of the narrow part of the corolla-tube, large, triangular, with two well-marked lateral lobes, almost blocking the entrance of the corolla-tube. *Stamens* subequal, much exserted, free from the corolla above the insertion of the scales. *Style* usually glabrous. Each *nutlet* somewhat pointed at the apex; with three well-marked longitudinal ridges; with the surface covered with rather small tubercles which become larger on the ridges.

Habitat. Somewhat sheltered places on lower mountain slopes; frequently near water.

Flowering season. July to October.

CERES: Mitchell's Pass, *Kolbe* 14382 in Herb. Bolus! CAPE: Orange Kloof, *Schlechter* 738! PAARL: French Hoek Valley! WORCESTER: Hex River

Valley, *Bolus* 2897 ! LADISMITH : Ladismith, *Levyns* 2093 ! *Levyns* 2095 ! *Levyns* 2320 ! Seven Weeks' Poort, *Phillips* 1557 ! *Levyns* 2494 ! WITHOUT LOCALITY : *Thunberg* ! *Masson* !

Note.—Schinz has recently named a specimen, Schlechter 785, *Lobostemon Wrightii* (16). In my opinion, however, this plant is probably a hybrid between *L. paniculatus* Buek and *L. trichotomus* DC., my reasons for holding this view being as follows :—The specimen in question was collected in June 1892 on Table Mountain (alt. 2,300 feet). During May of the same year Schlechter had collected in Orange Kloof on Table Mountain (alt. 900 feet) a plant which, although rather far advanced in its flowering season, agrees with specimens of *L. paniculatus* Buek. Schlechter 785 has the general habit of *L. paniculatus*, but the corolla is intermediate between that of *L. paniculatus* and that of *L. trichotomus*. The fruits are very like those of *L. trichotomus*. *L. trichotomus* has been recorded from Orange Kloof, and a personal knowledge of the distribution of species of *Lobostemon* on Table Mountain inclines me to the belief that Schlechter 785 must have been collected in the neighbourhood of Orange Kloof.

3. LOBOSTEMON HORRIDUS Levyns, sp. n. ; ramis simplicibus erectis ; foliis lanceolatis aut ovato-lanceolatis, marginibus crassis et setiferis ; inflorescentia paniculata senectuti ; calycis lobis aequalibus brevibus setulosis ; corolla regulari aut lobis paulum inaequalibus hypocrateriformi coerulea ; squamis triangulatis magnis ; staminibus fere aequalibus exsertis.

A stiff shrub, about 80 cm. high, branching at the base and then not again till just below the inflorescence. *Branches* setose, with coarse and fine bristles mixed. *Leaves* lanceolate to ovate-lanceolate, sometimes linear on young vigorous shoots, acute or somewhat obtuse, reaching about 4 cm. in length and 7 mm. in width, with a prominent midrib on the under surface and thickened margin, armed with stout spines along the projecting midrib and on the margin, with smaller spines on the lower surface and a few on the upper surface. *Inflorescence* cymose, cymes elongating greatly in the fruiting stage. Bracts not larger than the flowers, similar to the leaves in texture and spininess, but smaller and ovate. *Calyx* about as long as the cylindrical portion of the corolla-tube ; sepals equal, elliptic-oblong, somewhat obtuse, spine-tipped and armed with bristles. *Corolla* with a narrow cylindrical tube about one-third the total length of the corolla ; upper portion spreading outwards rather abruptly, regular, or with two lobes very slightly larger than the rest ; less than 1 cm. in length ; glabrous outside or with a few scattered bristly hairs ; blue. *Staminal scales* inserted at the entrance of the narrow part of the corolla-tube, large, triangular with two lateral basal lobes. *Stamens* rather unequal, one being definitely shorter than the rest, much exserted, free from the corolla above the insertion of the scales. *Style* glabrous. Each *nutlet* somewhat pointed at the apex, with three well-developed longitudinal ridges ; the surface tuberculate, the tubercles most prominent on the ridges.

Habitat. Mountains at high altitudes, round the margin of the karoo.

Flowering season. Insufficiently known. Has been collected in flower in April.

WORCESTER : top of the Witteberg near Whitehill, *Compton* 2971 ! *Levyns* 2881 !

4. LOBOSTEMON GRACILIS Levyns, sp. n. ; caule ramoso ; foliis linearibus vix strigosis ; inflorescentia paniculata senectuti ; calycis lobis aequalibus brevibus strigosis ; corolla paulum inaequali hypocrateriformi extus paulum puberula coerulea aut alba ; squamis triangulatis magnis ; staminibus sub-aequalibus exsertis.

A branched shrub up to 1 m. in height. *Branches* strigose. *Leaves* spreading, linear, acute or sub-obtuse, with the midrib not or hardly projecting on the under surface, up to 4 cm. long and 3 mm. wide, minutely strigose on both surfaces, hairs visible only under magnification ; marginal hairs enlarging with age ; true green in colour. *Inflorescence* cymose ; cymes rather dense when young, but elongating with age. *Bracts* not larger than the flowers, of the same general texture and hairiness as the leaves, but smaller ; youngest bracts ovate, oblique. *Calyx* about as long as the cylindrical portion of the corolla-tube ; sepals equal, linear, obtuse or acute, densely strigose. *Corolla* with a narrow cylindrical tube about two-fifths of its total length ; upper portion spreading outwards rather abruptly, slightly zygomorphic owing to two lobes being larger than the rest, about 1 cm. long, with a few scattered hairs outside ; blue or white. *Staminal scales* inserted at the entrance of the narrow tubular portion of the corolla, large, triangular with two well-developed lateral lobes, directed outwards and upwards, almost blocking the entrance of the corolla-tube. *Stamens* subequal, one, placed between the two larger corolla-lobes, rather shorter than the rest, much exserted, free from the corolla above the insertion of the scales. *Style* glabrous. Each *nutlet* rather pointed, with three well-developed longitudinal ridges ; rugose-tuberculate, with the tubercles best developed along the ridges.

Habitat. A sandstone kopje.

Flowering season. September to October.

ROBERTSON : *Levyns* 2776 !

5. LOBOSTEMON CAPITATUS Buek in Linnaea, xi, p. 143 (1837) ; DC. Prod. x, p. 12 (1846) ; C. H. Wright in Fl. Cap. iv, 2, p. 37 (1904) ; *L. sphaero-cephalus* Buek in Linnaea, xi, p. 143 ; DC. Prod. x, p. 12 ; C. H. Wright in Fl. Cap. iv, 2, p. 36. *L. cephaloideus* DC. Prod. x, p. 12 ; C. H. Wright in Fl. Cap. iv, 2, p. 42. *L. capitiformis* DC. Prod. x, p. 12 (1846). *Echium hispidum* Burm. Prod. Cap. p. 5 (1768). *E. capitatum* Linn. Mant. p. 42 (1770) ; Lam. Ill. p. 414, no. 1869 (1791) ; Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. t. i, 2, p. 785 (1798) ; Pers. Syn. i, p. 163 (1805) ; Lehm. Pl. Asper. p. 430 (1818) ; Roem et Schult. Syst. Veg. iv, p. 13 (1819) ; Lehm. Ic. t. xxvii (1821) ; Thunb. Fl. Cap. ed. Schult. p. 166 (1823) ; Drège, Zwei Pflanzengeogr. Documente, p. 102 (1843). *E.*

sphaerocephalum Vahl. Symb. iii, p. 22 (1794) ; Lehm. Pl. Asper. p. 431 (1818) ; Roem. et Schult. Syst. Veg. iv, p. 715 (1819) ; Lehm. Ic. t. xxviii (1821) ; Drège, Zwei Pflanzengeogr. Documente, p. 118 (1843). *E. capitiforme* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 51 (1924). *E. cephaloideum* I. M. Johnston, *l. c.* p. 52.

An undershrub, sometimes almost herbaceous, but always with a woody base, moderately branched, about 60 cm. in height or less. *Branches* covered with numerous, weak, scattered hairs, some small and some much longer. *Leaves* usually more or less spreading, occasionally imbricate, lanceolate, or linear, usually acute, from 2 to 5 cm. in length and about 8 mm. in width, but very variable in size, covered with scattered hairs standing out from the surface, the hairs being more abundant and coarser on the lower surface. *Inflorescence* cymose, cymes somewhat numerous, compact or spreading, elongating with age. *Bracts* similar to the leaves, but broader and smaller. *Calyx* about the length of the narrow portion of the corolla-tube or a little longer ; sepals equal, linear, covered outside with upwardly directed bristles, the bristles being finer, longer, and more numerous towards the base. *Corolla* with a narrow cylindrical tube about half the total length, upper portion spreading outwards rather abruptly, regular, usually less than 5 mm. in length, glabrous outside ; lobes usually oblong, frequently a rather faded brown at the tip, but white towards the base, often with a purple keel on each lobe, slightly scented. *Staminal scales* inserted near the top of the narrow portion of the corolla-tube, bluntly triangular with small side-lobes, almost blocking the throat of the corolla. *Stamens* equal or nearly so, much exserted, adnate to the corolla for a very short distance above the insertion of the scales. *Style* glabrous or nearly so. Each *nutlet* rather pointed with three longitudinal ridges, strongly tuber-culate, and slightly rugose, with very short bristles on the tops of the tubercles.

Habitat. Flats and lower mountain slopes.

Flowering season. September to October.

PIQUETBERG : Piquetberg, *Bolus* ! Twenty Four Rivers, *Zeyher* ! MALMES-BURY : Groenkloof, *Drège* ! *Pappe* ! *Ecklon and Zeyher* ! Mamre, *Bolus* 4320 ! Compton 3716 ! *Levyns* 3283 ! *Levyns* 2447 ! Darling, *Bolus* 12775 ! Hopefield, *Bachmann* 1240 ! TULBAGH : *Ecklon and Zeyher* ! CAPE : between Tygerberg and Simonsbay, *Drège* ! Kenilworth Race Course ; *Schlechter* 535 ! STELLEN-BOSCH : *Zeyher* ! WORCESTER : du Toit's Kloof, *Drège* 7853 ! WITHOUT LOCALITY : *Linnaeus* ! *Burmann* ! *Banks* ! *Roxburgh* ! *Auge* ! *Thunberg* ! *Drège* !

Note on nomenclature of L. capitatus Buek.

Echium hispidum Burm. is an older name than *Echium capitatum* L. How-ever, in the ' Prodromus ' de Candolle established *Lobostemon hispidus* for *Echium hispidum* Thunb., a very different plant. *Echium hispidum* Thunb. dates from 1794. While *Echium hispidum* Burm. was established in 1768, therefore there is no question as to which name has the priority. However, *E. hispidum* Thunb. was the species transferred to *Lobostemon* under that name, and therefore the

name *Lobostemon hispidum* is occupied. It is therefore proposed, in order to avoid further confusion, to retain the specific name *capitatus* for the plant named by Linnaeus, *Echium capitatum*, and to allow the name *Lobostemon hispidus* to be retained for Thunberg's *Echium hispidum*.

Note on *L. capitiformis* DC.

I have seen Drège 7853 from du Toit's Kloof, the specimen quoted by de Candolle. It differs from the typical *L. capitatus* Buek in the relatively broader, more closely packed leaves and more congested inflorescence. As in many species of *Lobostemon* this type of variation is common (see p. 407), I feel that there is no valid reason for retaining specific rank for this specimen.

6. LOBOSTEMON BOLUSII Levyns, sp. n. ; ramis simplicibus ; foliis ovatis aut ovato-lanceolatis, hispidis ; calycis lobis aequalibus brevibus hispidis ; corolla parva regulari hypocrateriformi extus glabra alba ; squamis late triangulatis ; staminibus fere aequalibus exsertis.

A scantily branched shrub, reaching 60 cm. in height. *Branches* with numerous weak hairs, coarse and fine mixed. *Leaves* usually loosely or closely imbricate, ovate-lanceolate or ovate, usually acute, averaging 1 cm. in length and 5 mm. in width, both surfaces covered with scattered spreading hairs, the hairs being more abundant and coarser on the lower surface, hairs on the lower surface eventually falling off and leaving conspicuous bulbous bases. *Inflorescence* cymose, the cymes often crowded, elongating with age. *Bracts* similar to the leaves, but smaller. *Calyx* about two-thirds or three-quarters the length of the narrow tubular portion of the corolla ; sepals equal, linear or linear-lanceolate, sub-obtuse or acute, covered outside with bristly hairs. *Corolla* with a narrow cylindrical tube, usually not more than one-third of the total length, widening rather abruptly in the upper portion, regular, 6 mm. in length or less, glabrous outside, colour usually white. *Staminal scales* inserted towards the top of the narrow portion of the corolla-tube, broadly triangular with small lateral lobes, almost blocking the entrance of the throat. *Stamens* equal or nearly so, much exserted, adnate to the corolla for a very short distance above the insertion of the scales. *Style* glabrous. *Fruit* not seen.

Habitat. Lower mountain slopes ; rather gravelly soil.

Flowering season. October.

STELLENBOSCH : Gordon's Bay, *Bolus* 8080 ! *Levyns* 2546 !

7. LOBOSTEMON TRICHOTOMUS DC. Prod. x, p. 11 ; C. H. Wright in Fl. Cap. iv, 2, p. 38. *L. verrucosus* Buek in Linnaea, xi, p. 139 ; DC. Prod. x, p. 8 ; C. H. Wright in Fl. Cap. iv, 2, p. 35. *L. breviflorus* DC. Prod. x, p. 10. *L. thymelaeoideus* DC. Prod. x, p. 11. *L. Wurmbii* DC. Prod. x, p. 11 ; C. H. Wright in Fl. Cap. iv, 2, p. 29. *Echium trichotomum* Thunb. Prod. p. 33 (1794) ; Thunb. in Schrad. N. Journ. i, 3, p. 39 (1806) ; Lehm. Pl. Asper. p. 433 (1818) ; Lehm. Ic. t. xxiv (1821) ; Drège, Zwei Pflanzengeogr. Documente, p. 108 (1843). *E. verrucosum* Lehm. Pl. Asper. p. 429 (1818) ; Lehm. Ic. t. xxxvii (1821) ; Thunb. Fl. Cap. ed. Schult. p. 164 (1823) ; Drège, Zwei Pflanzengeogr. Docu-

mente, p. 104 (1843). *E. canaliculatum* Drège, Zwei Pflanzengeogr. Documente, p. 70 (1843). *E. Wurmbii* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

The following are hybrids with *L. trichotomus* DC. as one of the parents :— *L. cinereus* DC. Prod. x, p. 10 ; C. H. Wright in Fl. Cap. iv, 2, p. 29. *Echium cinereum* I. M. Johnson, *l. c.*   *L. acutissimus* Buek in Linnaea, xi, p. 139 ; C. H. Wright in Fl. Cap. iv, 2, p. 29. *Echium acutissimum* I. M. Johnston, *l. c.* p. 51.

A branched shrub, 1 m. high or less. *Branches* covered with adpressed hairs, which are sometimes dense and silvery. *Leaves* acute or obtuse, linear or linear-lanceolate, from 1 to 5 cm. long, 5 mm. wide or less, showing great variability in size ; degree of hairiness also variable, ranging from the type with scattered adpressed hairs to the type with dense silvery indumentum ; all forms becoming less hairy with age ; leaves ascending when young, usually crowded. *Inflorescence* of a few or several cymose branches. *Bracts* similar to the leaves, but smaller, and becoming ovate-lanceolate in the upper parts of each cyme. *Calyx* a half to a third as long as the corolla ; sepals linear ; equal or nearly so ; moderately or densely hairy outside. *Corolla* usually with a marked cylindrical basal portion which after a short distance begins to widen gradually ; two posterior lobes usually larger than the rest ; rarely all the lobes equal ; from 1 to 2 cm. in length ; glabrous or hairy outside ; usually blue, less often pink. *Staminal scales* inserted about one-quarter or one-third of the way up the tube, well developed, somewhat triangular, with small lateral lobes at the base. *Stamens* slightly unequal in size ; slightly adnate to the corolla above the insertion of the scales ; exserted or just included. *Style* glabrous or hairy. Each *nutlet* with one median and two lateral longitudinal ridges ; rugose-tuberculate ; tubercles especially pronounced on the ridges.

Habitat. Sandy soil ; flats and mountains, reaching about 5,500 feet in the Cederberg. Much eaten by sheep.

Flowering season. August to November.

CALVINIA : between Grasberg River and Watervals River, *Drège*! CLAN-WILLIAM : Pakhuisberg, *MacOwan* 3260! *Schlechter* 8654! Cederberg, *Bodkin* 9063 in Herb. Bolus! *Levyns* 2967! *Barnard* 44135 in Mus. Austr. Afr.! Koudeberg, *Schlechter* 8736! Wupperthal, *Drège* 7845! Modderfonteinsberg *Drège*! Ezelsbank, *Drège* 7846 *b*! Algeria, *Levyns* 2187! Clanwilliam, *Diels* 790! *Leipoldt*! Zeekoe Vlei, *Levyns* 2577! Giftberg, *Drège* 7846 *c*! *Marloth* 2654! *Phillips* 7468! Biedouw, *Leipoldt* 579! Oliphants River Mountains, *Stephens* 6877! PIQUET-BERG : *Niven* 19! *Schlechter* 5189! *Bolus* 13615! *Penther* 1814! *Rogers* 131! CERES : Michell's Pass, *Schlechter* 8941! Ceres, *Rogers* 28706! Zwart Ruggens, *Marloth* 3285! *Levyns* 1915! *Levyns* 1794! *Levyns* 1855! Cold Bokkeveld, *Marloth* 10651! *Levyns* 1949! *Levyns* 1944! *Levyns* 1945! Bonteberg, *Compton* 3741! TULBAGH : *Pappe*! *Bolus* 5209! *Drège* 7846 *a*! *Thom* 1206! *Levyns* 2552! *Levyns* 2565! *Levyns* 2572! *Rogers* 17412! *Diels* 1022! *Bolus* 7584! *L. Bolus* 16750! *Bolus* 13614! *Ecklon and Zeyher*! *Hutchinson* 409! Nieuwe-kloof, *Schlechter* 7505! Witsenberg *Pappe*! CAPE : Orange Kloof, *Wolley Dod*

1648 ! between Rondebosch and Wynberg, *Burchell* 773 ! Retreat, *Rogers* 4749 ! Princess Vlei, *L. Bolus* 14017 ! Paradise Estate, Claremont, *L. Bolus* 16977 ! Ladies' Mile, Wynberg, *Purcell* 334 ! PAARL : Bains' Kloof, *Leipoldt* ! between Durbanville and Wellington, *Levyns* 2526 ! WORCESTER : Brand Vlei, *Schlechter* 9941 ! WITHOUT LOCALITY : *Burmann* ! *Sieber* ! *Ecklon* ! *Lehmann* ! *Thunberg* ! *Ecklon and Zeyher* ! *Scholl* 316 ! *Oldenburg* ! *Roxburgh* ! *Drège* 7846 *d* !

The following are hybrids :—

CLANWILLIAM : between Heerenlogement and Kanagas Berg, *Drège* ! Zeekoe Vlei, *Schlechter* 8489 ! CERES : *Marloth* 6371 *a* ! TULBAGH : Tulbagh Kloof, *Ecklon and Zeyher* ! CAPE : Wynberg, *Bolus* 2897 ! *Ecklon and Zeyher* 4789 ! *Thunberg* !

8. LOBOSTEMON HISPIDUS DC. Prod. x, p. 10 ; C. H. Wright in Fl. Cap. iv, 2, p. 42. *L. glaber* Buek in Linnaea, xi, p. 137 ; DC. Prod. x, p. 5 (partly) ; C. H. Wright in Fl. Cap. iv, 2, p. 28 (partly). *L. Swartzii* Buek in Linnaea, xi, p. 137 ; DC. Prod. x, p. 5 (partly) ; C. H. Wright in Fl. Cap. iv, 2, p. 29 (partly). *Echium hispidum* Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. t. i, 2, p. 784 (1798) ; Pers. Syn. Pl. i, p. 163 (1805) ; Thunb. in Schrad. n. Journ. i, 3, p. 40 (1806) ; Lehm. Pl. Asper. p. 433 (1818) ; *E. glabrum* Vahl. Symb. iii, p. 22 (1794) ; Lehm. Pl. Asper. p. 427 (1818) ; Lehm. Ic. t. xxvi (1821). *E. Swartzii* Lehm. Pl. Asper. p. 426 (1818) ; Lehm. Ic. t. xvi. (1821) ; Roem. et Schult. Syst. Veg. iv, p. 714 (1819) ; Drège, Zwei Pflanzengeogr. Documente. *E. verrucosum* Drège, Zwei Pflanzengeogr. Documente, p. 104.

A moderately branched undershrub, about 60 cm. in height. *Branches* when young covered with short hairs, interspersed with a few much longer hairs. *Leaves* acute or obtuse, linear or linear-lanceolate, variable in size, from 1 to 3 cm. long and 2 to 5 mm. wide, hispid with stiff scattered hairs on both surfaces, hairs not adpressed to the leaf-surface. *Inflorescence* of few to several cymose branches. *Bracts* similar to the leaves, but smaller. *Calyx* less than half as long as the corolla ; sepals approximately equal, linear, outer surface covered with stiff bristly hairs. *Corolla* widening gradually, funnel-shaped, with two posterior lobes larger than the rest, 1·0 to 1·5 cm. long, glabrous outside, usually white, but sometimes blue or pink, frequently with well-marked pink veins. *Staminal scales* inserted rather more than one-third of the way up the tube, well developed, broadly triangular with two small lateral lobes. *Stamens* of three lengths, but the differences in length not pronounced, included or just exserted, hardly adnate to the corolla above the insertion of the scales. *Style* with a few scattered hairs or almost glabrous. Each *nutlet* with a beak-like apex, median and lateral ridges well developed, whole surface tuberculate-rugose, the columnar tubercles specially developed on the lateral ridges, tufts of glassy spicules scattered over the surface.

Habitat. Clay soils of rhenosterveld and hills of Witteberg sandstone round the borders of the karoo.

Flowering season. August to November.

CERES : Cold Bokkeveld, *Marloth* 10634 ! MALMESBURY : Zwartland, *Zeyher* 1245 ! Hopefield, *Schlechter* 5319 ! Moorreesburg, *Levyns* 2998 ! TULBAGH : near Saron, *Schlechter* 8459 ! CAPE : near Tygerberg, *Bergius* ! *Levyns* 1963 ! between Koeberg Road and Melkbosch Strand, *Pillans* 18793 in Herb. Bolus ! Lion Mountain, *Drège* ! Constantia ! PAARL : between Durbanville and Wellington, *Levyns* 2395 ! *Levyns* 3183 ! *Levyns* 3182 ! *Levyns* 3184 ! Dal Josaphat, *Tyson* 869 ! Wellington, *Grant* 2365 ! Groot Drakenstein and at the foot of Paarl Mountain, *Drège* ! between Hermon and Tulbagh, *Levyns* 2563 ! *Levyns* 2564 ! WORCESTER : Tweedside, *Compton* 3192 ! *Levyns* 2358 ! *Levyns* 2772 ! *Levyns* 2769 ! *Levyns* 2770 ! Matroosberg, *Davidson* 43 ! WITHOUT LOCALITY : *Thunberg* ! *Thom* ! *Zeyher* 1244 ! *Drège* ! *Leipoldt* !

Note 1.—Much confusion has existed in the past with regard to *Lobostemon glaber* Buek. In 1794 Vahl established *Echium glabrum*, which he described as differing from *E. laevigatum* in having narrower leaves, hairy branches, a hairy calyx, and smaller flowers. His description is vague and would fit equally several allied species. Lehmann some years later adopted Vahl's name for a plant which he described and figured. His description suggests that the plant to which he referred was the plant now called *Lobostemon hispidum* DC. ' Corolla irregularis alba, majuscula ' fits that species well. On the other hand, Lehmann's figure agrees better with the plant known as *Lobostemon paniculaeformis* DC. Buek in 1837 transferred the species to the new genus *Lobostemon* as *L. glaber* Buek, and quoted a specimen among Ecklon's plants collected ' in terra Zwartland '. This specimen is probably ' Zeyher 1245, Zwartland ' to which reference is made below. De Candolle complicated matters further by quoting as examples of this species a specimen collected by Ecklon on Table Mountain (=*L. glaucophyllus* Buek), and one of Drège from the Onderbokkeveld (=*L. Pearsonii*, sp. n.). In the ' Flora Capensis ' C. H. Wright quoted several specimens belonging to other species, chiefly *L. glaucophyllus* Buek.

In the same year that Vahl founded *Echium glabrum*, Thunberg established *Echium hispidum*. The type-specimen of this at Uppsala is undoubtedly the same plant as Zeyher 1245. Further, Thunberg's name is appropriate, while Vahl's is not. The species of the former has a better claim to recognition than Vahl's, and I propose to retain *L. hispidus* (Thunb.) DC. and reduce *L. glaber* to a synonym.

Note 2.—*Echium Swartzii* was established by Lehmann in 1818. His descriptions and figures are somewhat inadequate, but there is nothing to prevent our acceptance of Buek's interpretation of the species when he transferred it to *Lobostemon* as *L. Swartzii*, and quoted two of Ecklon's specimens as types. I have seen one of these, that from Constantia, which is now in the Herbarium of the South African Museum. In view of the general accuracy of Buek's work it may be assumed that the other specimen agreed with this. This plant is the common form of *L. hispidus* DC., and therefore *L. Swartzii* Buek becomes

a synonym of that species. De Candolle and C. H. Wright included forms of *L. glaucophyllus* Buek under this species.

Note 3.—There are two distinct forms of *L. hispidus* DC., which appear growing together over the whole area occupied by the species. Thunberg's type-specimen and Zeyher 1245 (at Kew and at Vienna) belong to the less common form, while two other specimens bearing the number Zeyher 1245 (at the British Museum and at the South African Museum) belong to the common form. For reasons given elsewhere I consider that these two forms are merely varieties of a single species—*L. hispidus* DC. Buek, whose admirable work on *Lobostemon* gives evidence throughout of his strong feeling for natural affinities, does not apply the name *L. hispidus* to any species, but he describes in successive paragraphs the two species *L. glaber* and *L. Swartzii*. Buek's arrangement throughout is a phylogenetic one and the juxtaposition of these two species cannot be regarded as accidental. *L. glaber* Buek is probably the less common form of *L. hispidus* DC. (The only specimen I have seen of Zeyher 1245 bearing the legend ' Zwartland ' is that at Kew, and it is this form.) *L. Swartzii* Buek is probably the common form of the species.

9. Lobostemon paniculaeformis DC. Prod. x, p. 8 ; C. H. Wright in Fl. Cap. iv, 2, p. 35. *Echium paniculatum* Drège, Zwei Pflanzengeogr. Documente, p. 180 ; not of Thunb. or Lehm. *E. paniculaeforme* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A rather dense shrub a little less than 1 m. in height. Young *branches* covered with short hairs, interspersed with some much longer ones. *Leaves* mostly obtuse, oblong or oblong-lanceolate, 3 cm. long or less, and 6 mm. wide or less, upper surface glabrous or nearly so, lower surface and margin hispid with scattered hairs. *Inflorescence* cymose, cymes fairly densely aggregated towards the ends of the branches. *Bracts* similar to the leaves, but smaller. *Calyx* rather less than half the length of the corolla ; sepals equal or nearly so, linear, slightly hump-backed in profile, ciliate with stiff hairs and with a few similar hairs on the central vein and elsewhere on the outer surface. *Corolla* widening gradually with the two posterior lobes somewhat larger than the rest, funnel-shaped, about 1 cm. long, glabrous outside, usually blue. *Staminal scales* inserted rather more than one-third of the way up the tube, well developed, bluntly triangular, with two small lateral lobes. *Stamens* of three lengths, but the differences in length not very pronounced, included or just exserted, very slightly adnate to the corolla above the insertion of the scales. *Style* glabrous or nearly so. Each *nutlet* with a beak-like apex, median and lateral ridges well developed, whole surface tuberculate-rugose, the tubercles being specially developed on the lateral ridges, the largest tubercles conical, with very short glass-like spicules towards the apex of each.

Habitat. Flats. Chiefly on clay soils, but has been recorded on sand.
Flowering season. August to October.
Piquetberg : Witwater, *Bolus* 13616 ! Malmesbury : Groenekloof, *Drège* !

Darling, *Bolus*, 12776! *Bachmann* 562! *Levyns* 3190! *Levyns* 3244! between Malmesbury and Darling, *Lavis*! *Hutchinson* 202! between Malmesbury and Hopefield, *L. Bolus*! between Matjesfontein and Hazenkraal, *Bachmann* 1238! Moorreesburg, *Bolus* 9968! CAPE: near Koeberg Hotel, *Pillans* 18794 in Herb. Bolus! WITHOUT LOCALITY: *Zeyher* 141! *Ecklon and Zeyher*!

10. LOBOSTEMON LAEVIGATUS Buek in Linnaea, xi, p. 139; DC. Prod. x, p. 5; C. H. Wright in Fl. Cap. iv, 2, p. 28. *Echium laevigatum* Linn. Sp. Pl. ed. ii, p. 199 (1762); Lehm. Pl. Asper. p. 424 (1818); Lehm. Ic. t. iii (1821); Thunb. Fl. Cap. ed. Schult. p. 163 (1823).

A shrub branching at the base and then not again till just below the inflorescences, with a stiff upright habit ; in sheltered places reaching 1·7 m. in height, usually somewhat smaller : branches glabrous. *Leaves* sessile, usually acute, lanceolate or ovate-lanceolate, average size about 3·5 cm. long and 1·0 cm. wide, but in young vigorous shoots sometimes attaining a size of 10 cm. by 2·5 cm., glabrous except for stiff, white, bulbous-based hairs along the margin giving it a saw-like appearance, similar hairs occasionally scattered on either surface. *Inflorescence* cymose ; branches rather dense and short, elongating in the fruiting stage. *Bracts* similar to the leaves, but smaller. *Calyx* about half as long as the corolla, of five equal sepals ; sepals lanceolate, glabrous outside, except along the margin, which is fringed with stiff, upwardly directed hairs, occasionally with a few similar hairs outside. *Corolla* widening gradually, very slightly zygomorphic, about 1 cm. long, lobes somewhat oblong, not overlapping much at the base, glabrous outside, blue. *Staminal scales* inserted about one-third of the way up the tube, rather small, slightly pointed. *Stamens* of three lengths, exserted, all except the short stamen usually adnate to the corolla for a short distance above the insertion of the scales. *Style* with scattered hairs. *Fruit* not seen.

Habitat. Sandy places on mountains at fairly high altitudes. I have not found any undoubted examples of this species below an altitude of 4,000 feet.

Flowering season. Chiefly August to October.

CLANWILLIAM : Cederberg, *Drège*.! *Shaw* 5716 in Herb. Bolus! Koudeberg, *Schlechter* 8764! Ezelsbank, *Bolus* 9062! Elandsfontein, *Schlechter* 10033! *Cederberg*, Levyns 2880! CERES : Cold Bokkeveld, *Marloth* 10656! Zwart Ruggens, *Levyns* 1840! *Levyns* 1876! *Levyns* 1916! WITHOUT LOCALITY : *Thunberg*! *Tulbagh* 51 in Linn. Herb.!

The following are probably hybrids :—

CLANWILLIAM : Cederberg, *Drège*! *Schlechter* 8453! *Levyns* 2897! *Levyns* 3000! *Levyns* 2210! *Levyns* 2188! Olifants River Mountains, *Schlechter* 5082! *Schlechter* 5002! Modderfontein, *Schlechter* 7972! between Driefontein and Heerenlogement, *Pearson* 6736! Nardouw Kloof, *Pearson* 5415! *Pearson* 4948! PIQUETBERG : *Levyns* 2185! *Levyns* 2186! *Edwards* 132! Het Kruis, *Stephens and Glover*, 8779! CERES : Leeuwfontein, *Pearson* 3225! WITHOUT LOCALITY ; *Burmann*! *Drège*! *Ecklon and Zeyher*!

Note.—There are two specimens named *Echium laevigatum* in the Linnaean
Herbarium, and to these Daydon Jackson has assigned the numbers 15 and 16.
One of these specimens (Daydon Jackson 15), which was sent to Linné by
Tulbagh with his number 51, is a typical example of this species.   The other
specimen is quite different and is *L. glaucophyllus* Buek, a post-Linnaean species.
There is further evidence to show that Linné had not a clear conception of this
species.   In the ' Species Plantarum ' (ed. 2), under *Echium laevigatum*, he
refers to Plukenet's ' Mantissa,' xxxiii, t. 341.   The plant figured there bears
no resemblance to this species, and is much more like *L. montanus* Buek.

11. LOBOSTEMON GLAUCOPHYLLUS Buek in Linnaea, xi, p. 138 ; DC. Prod.
x, p. 5 ; C. H. Wright in Fl. Cap. iv, 2, p. 27.   *L. glaber* DC. Prod. x, p. 5 (partly);
C. H. Wright in Fl. Cap. iv, 2, p. 28 (partly).   *L. Swartzii* DC. Prod. x, p. 5
(partly) ;   C. H. Wright in Fl. Cap. iv, 2, p. 29 (partly).   *L. Drègei* DC. Prod.
x, p. 6.   *L. falcatus* Druce, Rep. Bot. Exch. Brit. Isles (1916) p. 633.   *Echium
glaucophyllum* Jacq. Ic. t. 312 (1786–1793) ; Andr. Rep. t. 165 (1801) ; Pers.
Syn. i, p. 163(1805) ; Drège, Zwei Pflanzengeogr. Documente, p. 67 (1843).
E. laevigatum Lam. Tabl. Encyc. i, p. 413 (1791).   *E. falcatum* Lam. Tabl.
Encyc. i, p. 413 (1791).   *E. glabrum* Thunb. Prod. p. 33 (1794) ; Thunb. Fl.
Cap. ed. Schult. p. 163 (1823).   *E. Swartzii* Drège, Zwei Pflanzengeogr. Docu-
mente, p. 180 (1843).   *E. Vahlii* Roem. et Schultes, Syst. Veg. iv, 1, p. 715 (1819).
E. papillosum Thunb. Fl. Cap. ed. i, 2, p. 8 (1811), not of Lehm.   *E. angusti-
folium* Fl. Cap. ed. Schult. p. 163 (1823).

The following is probably a hybrid with *L. glaucophyllus* Buek as one of
the parents :—*L. acutissimus* Buek in Linnaea, xi, p. 139 ; DC. Prod. x, p. 6 ;
C. H. Wright in Fl. Cap. iv, 2, p. 29.   *Echium acutissimum* I. M. Johnston in
Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A shrub reaching about 1 m. in height, branching moderately ; *branches*
glabrous.   *Leaves* acute or obtuse, lanceolate or linear-lanceolate, 6 cm. long
or less, rarely more than 1·7 cm. wide, somewhat fleshy, glaucous, glabrous,
except for stiff white bulbous-based hairs adpressed along the margin, on the
under side of the midrib, and sometimes scattered on the under surface as well.
Inflorescence cymose, not very dense, elongating somewhat in the fruiting
stage.   *Bracts* similar to the leaves, but smaller, upper ones almost ovate.
Calyx about half as long as the corolla or less ; sepals equal or nearly so,
lanceolate, mostly glabrous outside except along the margin, which is ciliate
with stiff, upwardly directed hairs, occasionally with a few scattered hairs
towards the apex.   Corolla widening gradually, funnel-shaped with well-
developed imbricate lobes, slightly zygomorphic or nearly regular, usually
about 1·5 cm. long, but sometimes reaching 2 cm. in length, glabrous outside,
usually blue, rarely pink.   *Staminal scales* inserted about one-quarter of the
way up the tube, broad, with a rounded apex. , *Stamens* of three lengths,
exserted or just included, all excepting the short stamen adnate to the corolla
for a very short distance above the insertion of the scales.   *Style* with scattered

hairs. Each *nutlet* with a beak-like apex and with a median and two lateral, not very prominent, ridges ; tuberculate in the lower part.

Habitat. Sandy places on the flats and on the lower mountain slopes.

Flowering season. Chiefly July to November.

NAMAQUALAND : *Scully* 1324 in Herb. Norm. Aust. Afr. ! *Scully* 124 ! *Bolus* 5715 ! *Bolus* 9427 ! *Morris* ! VAN RHYNSDORP : *Pritzel* ! Klaver, *Andreae* 496 ! Gift Berg, *Phillips* 7470 ! between Driefontein and Heerenlogement, *Pearson* 6736 ! CALVINIA : Van Rhyn's Pass, *Diels* 600 ! CLANWILLIAM : Olifants River Mountains, *Schlechter* 5114 ! *Pearson* 7216 ! *von Schlicht* ! *Leipoldt*, 19863 in Herb. Bolus ! Modderfontein, *Schlechter* 7972 ! *Penther* 1815 ! Blaauwberg, *Drège* 7843 *b* ! Zeekoe Vlei, *Schlechter* 8574 ! *Phillips* 7469 ! Nardouw Mountain, *Diels* 383 ! Algeria, *Levyns* 3004 ! *Levyns* 2200 ! *Galpin* 10545 in Nat. Herb. Pretoria ! PIQUETBERG : *Levyns* 2170 ! *Bolus* ! Het. Kruis, *Stephens and Glover* 8779 (partly) ! CERES : Mitchell's Pass, *Grey* ! *Bolus* 2619 (partly) ! *Marloth* 6371 *b* ! MALMESBURY : Mamre, *Marloth* 6614 ! Vredenburg, *Levyns* 3243 ! TULBAGH : *Pappe* ! CAPE : Elsie's Peak, *Wolley Dod* 2936 ! Simonsbay, *Wright* ! *Milne* 139 ! *Jameson* ! *Schlechter* 1094 ! Fish Hoek, *Rogers* 16019 ! Muizenberg, *Levyns* 2402 ! Tokay, *Wolley Dod* 1273 ! between Rondebosch and Hout Bay, *Drège* ! Orange Kloof, *Hutchinson* 46 ! Camps Bay, *Zeyher* 44 ! *Burchell* 342 ! *Diels* 112 ! *Levyns* 2036 ! *Salter* 302 ! *Galpin* 4350 ! Tokai, *Gamble* 22137 ! CAPE Town, *Bolus* 2898 ! *Rehmann* 1557 ! *Knoop* 132 ! *Muir* 991 ! Table Mountain, *Ecklon* 257 ! *MacGillivray* 572 ! *MacOwan* 2684 ! *Rogers* 29496 ! *Pappe* ! Devil's Peak, *Bolus* 3724 ! *Krauss* ! *Wilms* 3461 ! *Pappe* ! *Marloth* 673 ! *Marloth* 1798 ! Cape Peninsula, *Rogers* 16960 ! Cape Flats, *Ecklon* 258 (partly), *Bolus* 5205 ! *Rehmann* 1989 ! Lion's Head, *Levyns* 2400 ! Wynberg, *Wolley Dod* 410 (partly) ! *Drège* 313 (partly) ! *Pappe* ! *L. Bolus* ! Kirstenbosch, *Levyns* 1966 ! *Levyns* 1965 ! *Levyns* 1964 ! Tygerberg, *Levyns* 1962 ! PAARL : Paarlberg, *Prior* ! *Drège* ! *Drège* 7843 *a* ! French Hoek, *Phillips* 1241 ! *Levyns* 3447 ! STELLENBOSCH, *Ecklon and Zeyher* ! WORCESTER : Goudini Road, *Levyns* 1490 ! De Doorns, *Engler* 245 ! Hex River, *Tyson* 659 ! Fontainjesberg, *Stokoe* 18380 in Herb. Bolus ! Brandwacht valley, *Stokoe* 1288 ! ROBERTSON : Montagu, *Page* 82 ! WITHOUT LOCALITY : *Thunberg* ! *Alexander Prior* ! *Forbes* 91 ! *Zeyher* ! *Lehmann* ! *Scholl* ! *Drège* ! *Wawra* 12 ! *Sieber* ! *Breutel* ! *Bergius* ! *Mund and Maire* ! *Lalande* ! *Ecklon* ! *Harvey* 229 ! *Burmann* ! *MacWilliam* ! *Verreaux* ! *Burmann* 31 ! *Linné* !

The following are probably hybrids :—

NAMAQUALAND : Steinkopf, *Meyer* 7 ! VAN RHYNSDORP : Heerenlogement, *Drège* ! Klaver, *Andreae* 513 ! CLANWILLIAM : Olifants River Mountains, *Schlechter* 5082 ! *Schlechter* 5002 ! between Driefontein and Heerenlogement, *Pearson* 6736 ! Cederberg, *Levyns* 2897 ! *Levyns* 3000 ! *Levyns* 2210 ! *Levyns* 2188 ! Modderfontein, *Schlechter* 7972 (partly) ! Clanwilliam, *Drège* ! Zeekoe Vlei, *Levyns* 1234 ! Ezelsbank, *Drège* ! PIQUETBERG : *Edwards* 132 ! *Levyns* 2185 ! *Levyns* 2186 ! Het Kruis, *Stephens and Glover* 8779 (partly) ! CERES : Mitchell's Pass, *Bolus* 2619 ! *Schlechter* 9851 ! between Tulbagh and Hantam,

Thom! MALMESBURY : near Moorreesburg, *Bolus* 9969 ! CAPE : Wynberg, *Burchell* 878 ! *Wolley Dod* 2018 ! *Wolley Dod* 410 (partly) ! *Wilms* 3465 ! *Drège* 313 (partly) ! *Bolus* 2897 ! *Ecklon* 4789 ! Kirstenbosch, *Levyns* 2779 ! *Levyns* 1971 ! *Levyns* 1972 ! *Levyns* 1970 ! *Levyns* 2032 ! Diep River, *Marloth* 7192 ! STELLENBOSCH : *Ecklon and Zeyher* ! WITHOUT LOCALITY : *Lehmann* ! *Burmann* ! *Ecklon and Zeyher* !

Note.—All the plants from the neighbourhood of Worcester are peculiar. I have refrained from placing them in a separate species, as they approach *L. laevigatus* in floral structure, though not in general habit. Pending further information on the distribution of Lobostemons in this district, I have left these plants in *L. glaucophyllus* Buek. Possibly they are hybrids between that species and *L. laevigatus* Buek.

12. LOBOSTEMON HOTTENTOTICUS Levyns, sp. n. ; caule fruticoso simplice ; foliis lanceolatis aut anguste lanceolatis acutiusculis spinoso-ciliatis glabriusculis ; calycis lobis aequalibus, corolla dimidio brevioribus ciliato-setosis ; corolla infundibuliformi extus glabra alba aut rubra pallida ; squamis orbiculatis ; staminibus inaequalibus inclusis aut breviter exsertis.

An undershrub about 60 cm. high, branching occasionally. *Branches* glabrous or with a few bristly hairs. Leaves sessile, usually acute, lanceolate or linear-lanceolate, from 2 to 5 cm. long, rarely more than 8 mm. wide, variable in size, sometimes nearly glabrous, but usually with stiff bristles along the margins, on the midrib, and also sometimes on the under surface. *Inflorescence* cymose, few- to many-flowered, elongating in the fruiting stage. Bracts similar to the leaves, but smaller ; upper bracts ovate ; marginal bristles usually well developed. *Calyx* about half as long as the corolla ; sepals approximately equal in size, lanceolate, ciliate, with stiff bristles, and often with similar bristles along the upper part of the median vein. *Corolla* funnel-shaped, widening gradually from a narrow base ; lobes well developed, slightly zygomorphic ; about 2 cm. long or less, glabrous outside, pale pink or white. *Staminal scales* inserted about one-quarter or one-third of the way up the tube, small, with a rounded apex. *Stamens* of three lengths, exserted or just included, adnate to the corolla for a very short distance above the insertion of the scales. *Style* with scattered hairs. Each *nutlet* with three longitudinal ridges, strongly tuberculate except at the apex.

Habitat. Lower mountain slopes ; gravelly soil.

Flowering season. July to October.

STELLENBOSCH : Somerset West, *Levyns* 2527 ! Sir Lowry's Pass, *Kuntze* ! *Diels* 1222 ! *Page and Guthrie* ! *Ecklon and Zeyher* ! *Levyns* 2037 ! *Levyns* 2538 ! *Rogers* 26648 !

13. LOBOSTEMON PEARSONII Levyns, sp. n. ; *L. glaber* DC. Prod. x, p. 5 (partly) ; C. H. Wright in Fl. Cap. iv, 2, p. 28 (partly). *Echium glabrum* Drège, Zwei Pflanzengeogr. Documente, p. 70 ; caule ramoso ; foliis lineari-lanceolatis acutis glabris margine et subtus ad costam setis basi minute tuberculatis

instructis ; calycis lobis aequalibus aut subaequalibus ciliatis et paucis pilis, corolla fere dimidio brevioribus ; corolla paulum inaequali extus glabra saepe coerulea ; squamis orbiculatis ; staminibus inaequalibus breviter exsertis.

A shrub about 1 m. in height, branching moderately, rather less divaricately so than *L. glaucophyllus* Buek. *Branches* glabrous. *Leaves* acute, narrowly lanceolate, 7 cm. long in luxuriant specimens, frequently much shorter, 7 mm. wide or less, glabrous except for stiff, white, bulbous-based hairs adpressed to the margin, sometimes scattered along the midrib and near the apex on the under surface. *Inflorescence* cymose, not very dense. *Bracts* similar to the leaves, but smaller, upper ones almost ovate. *Calyx* usually less than half the length of the corolla ; sepals equal or nearly so, ciliate with stiff white hairs, with a few similar hairs scattered on the outer surface. *Corolla* funnel-shaped, widening gradually, slightly zygomorphic, varying from 1·5 cm. to under 1 cm. in length, glabrous outside, usually blue, but occasionally pink or white. *Staminal scales* inserted about one-quarter or one-third of the way up the tube, rather variable in size, usually small and rounded at the apex. *Stamens* of three lengths, usually just exserted. *Style* with scattered hairs. Each *nutlet* with a beak-like apex and a well-developed median ridge, with the lateral ridges weakly developed, tuberculate in the lower part.

Habitat. Rocky kopjes and lower mountain slopes.

Flowering season. August to November.

NAMAQUALAND : Khamiesberg, *Pearson* 5889 ! *Pearson* 5009 ! *Pearson* 6271 ! *Drège* ! Riet Kloof Mountains, *Pearson* 5715 ! Pedros Kloof and Lilyfontein, *Drège* ! CALVINIA : Onderbokkeveld, *Drège* ! between Grasberg River and Waterval River, *Drège* ! Hantam Mt., *Meyer* ! WORCESTER : Osplaats, *Rogers* 16704 ! Tweedside, *Levyns* 2355 ! *Levyns* 2361 ! *Compton* 3189 ! *Compton* 3191 ! Touws River, *Levyns* 870 ! Pieter Meintjes, *Marloth* 10786 ! Tafelberg, *Pillans* 14158 in Herb. Bolus ! ROBERTSON : Cogman's Kloof, *Tredgold* 431 !

The following are probable hybrids :—

NAMAQUALAND : Khamiesberg, *Pearson* 6369 ! CLANWILLIAM : Nardouw Kloof, *Pearson* 5415 ! *Pearson* 4948 ! CERES : Leeuwfontein, *Pearson* 3225 ! WORCESTER : Touws River, *Schimper* !

14. LOBOSTEMON STACHYDEUS DC. Prod. x, p. 7 ; C. H. Wright in Fl. Cap. iv, 2, p. 33. *L. ferocissimus* DC. var. *albicalyx* C. H. Wright in Fl. Cap. iv, 2, p. 34. *Echium* sp. Drège, Zwei Pflanzengeogr. Documente, p. 62. *E. stachydeum* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A divaricately branched shrub, about 60 cm. high. *Branches* densely hairy, with stiff spiny hairs scattered amongst softer weak hairs. *Leaves* linear or linear-lanceolate, acute, with revolute margins, and with a prominent midrib on the under surface, up to 9 cm. in length in well-developed specimens, but usually less, 1 cm. wide or less, hairy on both surfaces, with fine hairs and coarse bristles mixed, with spiny bristles well developed on the margin and the lower side of the midrib. *Inflorescence* a pseudo-spike, consisting of numerous cymules

in the axils of bracts, each cymule, as a rule, reduced to two flowers. *Bracts* similar to the leaves, becoming smaller and ovate-lanceolate towards the apex ; lower bracts larger than the flowers in their axils. *Calyx* rather less than one-third the length of the corolla, globose with acute lobes converging inwards ; sepals equal or nearly so, joined for rather less than one-half of their length, covered with a mixture of fine and coarse hairs, each lobe armed with a few spiny bristles. *Corolla* consisting of a narrow tube at the base, then widening gradually, two posterior lobes larger than the rest, about 12 mm. in length or less, glabrous outside except for stiff hairs along the median vein of each lobe and along the margins, blue, shading to deep pink at the base. *Staminal scales* inserted rather less than one-third of the way up the tube, hardly more than small ridges. *Stamens* of three lengths, all but the short one exserted, adnate to the corolla for a short distance above the insertion of the scales, the short stamen the least adnate. *Style* hairy. Each *nutlet* rugose-tuberculate, median and lateral ridges inconspicuous.

Habitat. Sandy mountain slopes.

Flowering season. October to December.

NAMAQUALAND : Khamiesberg, *Pearson* 5916 ! *Pearson* 5780 ! *Pearson* 5890 ! *Drège* 3091 ! between Pedros Kloof and Lilyfontein, *Drège* ! LADISMITH : Seven Weeks' Poort, *Phillips* 1555 ! *Levyns* 2342 ! BEAUFORT WEST : Nieuw-veld, *Drège* 7849 ! GEORGE : Kamanassie Mountains, *Alexander* ! GRAAFF REINET : Oudeberg, *Bolus* 155 ! WITHOUT LOCALITY : *Masson* ! *Drège* ! *Bowie* ! *Rogers* 49073 !

Note.—Bowie quotes a locality for this, as in most other specimens of his, but the information is so obviously wrong that I have refrained from quoting his localities.

15. LOBOSTEMON ARGENTEUS Buek in Linnaea, xi, p. 133 ; DC. Prod. x, p. 7 ; C. H. Wright in Fl. Cap. iv, 2, p. 30. *L. Zeyheri* Buek in Linnaea, xi, p. 134 ; DC. Prod. x, p. 6 ; C. H. Wright in Fl. Cap. iv, 2, p. 33. *L. ferocissimus* DC. Prod. x, p. 7 ; C. H. Wright in Fl. Cap. iv, 2, p. 34 (excluding var. *albicalyx* C. H. Wright) ; *L. pilicaulis* C. H. Wright in Fl. Cap. iv, 2, p. 30. *L. montanus* Buek var. *minor* C. H. Wright in Fl. Cap. iv, 2, p. 31. *Echium argenteum* Bergius, Descr. Pl. Cap. p. 40 (1767) ; Roth. Bot. Abh. p. 63 (1787) ; Lam. Ill. p. 413, no. 1862 (1791) ; Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. i, 2, p. 783 (1798) ; Lam. Tabl. Encyc. i, p. 413 (1800) ; Andr. Bot. Rep. f. 154 (1801) ; Lehm. Pl. Asper. p. 421 (1818) ; Thunb. Fl. Cap. ed. Schult. p. 166 (1823). *E. ferocissimum* Andr. Bot. Rep. f. 39 (1801). *E. ferox* Pers. Syn. Pl. i, p. 163 (1805). *E. fruticosum* Jacq. Hort. Schoenbr. i. t. xxxiv (1797). *E. pilicaule* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A much-branched shrub 1 m. high or less. *Branches* densely covered with a mixture of fine and coarse hairs. *Leaves* oblong, lanceolate or ovate-lanceolate, mostly acute, with a prominent midrib on the lower surface, 5 cm. in length or less, 10 mm. in width or less, densely hairy with softer hairs generally

distributed, and coarse bristle-like hairs along the margin and on the midrib on the lower surface ; the bristles may be conspicuous or poorly developed ; softer hairs may be either adpressed or standing out from the leaf-surface. *Inflorescence* a pseudo-spike with one flower in the axil of each bract. *Bracts* similar to the leaves, but becoming smaller and more definitely ovate towards the apex of the inflorescence, most of the flowers exceeding the bracts. *Calyx* about half as long as the corolla or less ; sepals acute, unequal, the two lateral lanceolate and much larger than the rest, which are linear, covered with numerous hairs with which a few bristles are mixed. *Corolla* funnel-shaped, widening gradually, distinctly zygomorphic, the two posterior lobes much larger than the rest, 2 cm. long or less, glabrous outside or nearly so, though frequently with a few hairs fringing the lobes, usually deep blue. *Staminal scales* inserted a quarter of the way up the corolla-tube or less, small and rounded. *Stamens* of three different lengths, the shortest always included, the rest usually just included or exserted, all adnate to the corolla-tube above the insertion of the scales, the short stamen very shortly so. *Style* hairy. Each *nutlet* rugose-tuberculate, with three faintly developed, longitudinal ridges.

Habitat. Clay soils ; a common constituent of rhenosterveld.

Flowering season. November to January.

VAN RHYNSDORP : *Diels* 555 ! CLANWILLIAM : Twenty Four Rivers, *Ecklon and Zeyher* 1133 ! Citrusdal, *Levyns* 1353 ! PIQUETBERG : *Bolus* 13617 ! CERES : *Guthrie* 2196 ! MALMESBURY : Mamre, *Marloth* 8705 ! Hopefield, *Bachmann* 1239 ! Riebeek's Kasteel, *Drège* 1964 *b* ! TULBAGH : *Pappe* ! *Bolus* 5210 ! *Ecklon and Zeyher* ! *Levyns* 2576 ! *Marloth* 7116 ! *Schlechter* 7488 ! Ceres Road, *Schlechter* 9069 ! CAPE : near Roodebloem, *Bergius* ! Table Mountain, *Kuntze* ! *MacOwan* 2683 ! *Ryder* 159 ! *Muir* 1151 ! Lion's Mountain, *Ecklon* ! *Burchell* 141 ! *MacOwan* 1928 ! *Wolley Dod* 2329 ! *Bolus* 4508 ! *Ecklon* 256 ! *Levyns* 2401 ! Camps Bay, *Zeyher* 4844 ! *Salter* 302 ! *Alexander* ! *Levyns* 2042 ! Maitland, *Wolley Dod* 2164 ! Devil's Peak, *Pappe* ! Koeberg, *Pappe* ! Tygerberg, *Delessert* ! PAARL : between Drakenstein Mountain and Dal Josaphat, *Drège* 1964 *a* ! between Bain's Kloof and Wellington, *Hutchinson* 1069 ! CALEDON : Genadendal, *Alexander* ! Mountain ridges between Zwart berg and River Zonder Einde, *Zeyher* 1241 ! Bot River, *Levyns* 2276 ! Caledon, *Bolus* ! *Rogers* 29263 ! *Southey (Galpin* nos. 5038 and 5040) ! *Thorne* 45832 in Herb. Mus. Aust. Afr. ! WORCESTER : between Worcester and Villiersdorp, *Bolus* 5206 ! near Liefde, *Drège* 1964 *c* ! Bains Kloof, *Rogers* 29271 ! Eendragt, *Pica Survey* 931 ! BREDASDORP : Rietfontein Poort, *Bolus* 8579 ! *Schlechter* 9700 ! Elim, *Levyns* 3012 ! between Elim and Stanford, *Levyns* 3013 ! UNION-DALE : near Avontuur, *Bolus* 2429 ! HUMANSDORP : *Galpin* 4345 ! Essenbosch, *Fourcade* 861 ! UITENHAGE : Coega, *Rogers* 4583 ! Uitenhage, *Alexander* ! SOMERSET EAST : *MacOwan* 431 ! ALBANY : Grahamstown, *MacOwan* 431 ! *Britten* 5474 ! *Galpin* 240 ! Brak Kloof, *White* 94 ! Albany, *Drège* ! FORT BEAUFORT : *Cooper* 550 ! Kounap River, Adelaide, *Cooper* 545 ! WITH-OUT LOCALITY : *Thom* ! *Villette* ! *Drège* ! *Forster* ! *Lehmann* ! *Alexander* ! *Le*

Vaillant ! *Verreaux* ! *Pereheron* ! *Zeyher* ! *Thunberg* ! *Barber* ! *Masson* ! *Bojer* ! *Wawra* 188 ! *Pappe* ! *Boos* ! *Burmann* ! *Mund and Maire* ! *Lalande* ! *Malmaison* ! *Nelson* ! *Leipoldt* ! *Kolbe* ! *Sweet* ! *Bowie* !

The following is probably a hybrid :—

Camps Bay, *Zeyher* 4842 !

Note.—L. rosmarinifolius DC. is probably this species. There is no specimen of this in de Candolle's own herbarium, and I have seen no plant named thus in any other herbarium. The description of the calyx with two segments larger than the rest suggests that it is this species, as no other species has that character.

16. LOBOSTEMON FRUTICOSUS Buek in Linnaea, xi, p. 134 ; DC. Prod. x, p. 6 ; C. H. Wright in Fl. Cap. iv, 2, p. 31. *L. obovatus* DC. Prod. x, p. 10 ; C. H. Wright in Fl. Cap. iv, 2, p. 32. *L. lasiophyllus* DC. Prod. x, p. 10 ; C. H. Wright in Fl. Cap. iv, 2, p. 42. *Echium fruticosum* Linn. Sp. Pl. ed. i, 1, p. 139 (1753) ; Berg. Descr. Pl. Cap. p. 39 (1767) ; Mill. Dict. ed. 8, no. 7 (1768) ; Ait. Hort. Kew. ed. i. 1, p. 186 (1789) ; Lam. Ill. p. 413, no. 1865 (1791) ; Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. i, 2, p. 781 (1798) ; Bot. Reg. t. xxxvi (1815) ; Bot. Mag. t. 1772 (1816) ; Lehm. Pl. Asper. p. 420 (1818) ; Lehm. Ic. t. xxxviii (1821) ; Schult. Syst. Veg. iv, pp. 9 & 712 (1819) ; Thunb. Fl. Cap. ed. Schult. p. 165 (1823). *E. africanum* Pers. Syn. Pl. i, p. 163 (1805). *E. scabrum* Lehm. Pl. Asper. p. 362 (1818) ; Lehm. Ic. t. xxxv (1921) ; Thunb. Fl. Cap. ed. Schult. p. 166 (1823). *E. Bergianum* Drège, Zwei Pflanzengeogr. Documente, pp. 86, 99, 105 (1843). *E. spathulatum* Drège, Zwei Pflanzengeogr. Documente, p. 68, not of Viv. (1843). *E. lasiophyllum* Link. Enum. Berol. i, p. 170. *E. obovatum* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A branched shrub, 1 m. high or less. *Branches* densely hairy, with a mixture of fine and coarse hairs. *Leaves* oblanceolate, obovate or linear, obtuse or acute, from 1·5 cm. to 6 cm. in length and from 5 to 12 mm. wide, midrib prominent on the lower surface, both surfaces densely covered with adpressed hairs, rarely sparsely hairy. *Inflorescence* cymose, cymes somewhat short when young, but elongating with age. *Bracts* similar to the leaves in texture and hairiness, but linear or lanceolate and oblique. *Calyx* one-third to one-half the length of the corolla ; sepals linear, acute, covered with more or less adpressed hairs, one sepal usually smaller than the rest. *Corolla* funnel-shaped ; tube widening gradually, obliquely zygomorphic, up to 2·5 cm. long, shortly pubescent outside, blue, pink, or rarely white. *Staminal scales* inserted about one-fifth of the way up the tube, small and rounded, little more than transverse ridges. *Stamens* of three lengths, all more or less included, adnate to the corolla for a short distance above the scales, the short stamen very slightly adnate. *Style* hairy. Each *nutlet* with three longitudinal ridges, the median well developed, the lateral not prominent, rugose-tuberculate, tubercles rather prominent.

Habitat. Sandy places, usually at fairly low altitudes.

Flowering season. August to October.

NAMAQUALAND : *Morris* 5717 ! Spektakel, *Bolus* 9428 ! Ezelsfontein, *White-head* ! Leleifontein, *Drège* 3089 ! between Brakdam and Rietkloof, *Pearson* 5674 ! CLANWILLIAM : Olifant's River Valley, *Penther* ! PIQUETBERG : *Bolus* 13618 ! MALMESBURY : Hopefield, *Schlechter* 5189 ! *Bachmann* 2029 ! *Bachmann* 1237 ! *Bachman* 206 ! Darling, *Schlechter* 5338 ! *Bachmann* 564 ! between Kalabas Kraal and Malmesbury, *Hutchinson* 198 ! TULBAGH : *Schlechter* 8989 ! Tulbagh, *Diels* 995 ! CAPE : Table Mountain, *Ecklon* 255 ! *MacOwan* 2749 ! *MacOwan* 1636 ! *Drège* 7847 *a* ! *MacOwan* 816 ! *Dümmer* 150 ! *Ecklon and Zeyher* 84 ! *Engler* 43 ! *MacOwan* 2683 ! Devil's Peak, *Bolus* 3723 ! *Alexander* ! *Diels* 74 ! *Tyson* 2502 ! Cape Town, *Bolus* 2899 ! *Castelnau* 478 ! *Rehmann* 1556 ! *Wilms* 3462 (partly) ! *Knoop* 50 ! *Pappe* ! Rondebosch, *Zeyher* 4781 ! *Ecklon and Zeyher* 3451 ! Claremont, *Verdoorn* ! Groote Schuur, *Wolley Dod* 629 ! Kirsten-bosch, *Levyns* 2780 ! *Levyns* 1969 ! *Levyns* 1968 ! *Levyns* 1967 ! Wynberg, *Alexander* ! *Schenck* 607 ! Steenberg, *Verreaux* ! Simon's Bay, *MacGillivray* 571 ! *Jameson* ! Kalk Bay, *Rogers* 16197 ! Fish Hoek, *Rogers* 16008 ! Signal Hill, *Levyns* 2033 ! *Levyns* 2034 ! *Marloth* 7004 ! Clifton, *Smith* 2887 ! Camps Bay, *Zeyher* 81 ! *Levyns* 2035 ! Vygeskraal, *Wolley Dod* 1395 ! Philadelphia, *Levyns* 2575 ! PAARL : *Prior* ! *Wilms* ! Paarl Mountain, *Drège* 7847 *c* ! Berg River, *Drège* 7847 *b* ! STELLENBOSCH : *Sanderson* 978 ! *Levyns* 2030 ! *Schenck* 563 ! *Schenck* 590 ! *Levyns* 2031 ! *Penther* 1826 ! Mulder's Vlei, *Burtt-Davy* 12519 ! CALEDON : *Rogers* 28915 ! *Rogers* 28986 ! Onrust, *Drège* 3449 ! Hermanus, *Galpin* 4348 ! WORCESTER : Breede River, *Bolus* 2900 ! Brandt Vlei, *Bolus* 5207 ! Goudini Road, *Levyns* 1491 ! between Worcester and Wellington, *Levyns* 2388 ! Botha's Halt, *Pica Survey* 656 ! Brandwacht Valley, *Stokoe* 1271 ! Plateau on Fontainjesberg, *Stokoe* 18379 in Herb. Bolus ! ROBERTSON : *Levyns* 2775 ! BREDASDORP : Rietfontein, *Smith* 3163 ! SWELLENDAM, *Garnot* ! RIVERSDALE : Garcia's Pass, *Thorne* 43131 in Herb. Aust. Af. ! MOSSEL BAY : Cloete's Pass, *Muir* 1453 ! OUDTSHOORN : Olifant's River, *Gill* ! GEORGE, *Rogers* 11367 ! UNIONDALE : Zwartberg, *Bolus* 2430 ! WITH-OUT LOCALITY : *Linnaeus* ! *Bergius* ! *Burmann* 64 ! *Lalande* ! *Sieber* 92 ! *Lehmann* (partly) ! *Miller* ! *Zeyher* ! *Villette* ! *Wallich* ! *Elliot* ! *Forbes* ! *Harvey* 221 ! *Harvey* 227 ! *Thunberg* ! *Pappe* ! *Maude* ! *Perdonnet* 90 ! *Schinz* ! *Ecklon and Zeyher* 3449 ! *Scholl* ! *Drège* 336 ! *Banks* ! *Wawra* 166 ! *Zeyher* 215 ! *Krebs* ! *Meron* ! *Perrottet* ! *Jessen* ! *Gaudiehaud* !

The following is probably a hybrid :—

Camps Bay, *Zeyher* 4842 !

Note.—In the Linnaean Herbarium there are three specimens of this species (Daydon Jackson 1, 2, and 3). One of these has Tulbagh's number 98.

In Thunberg's Herbarium there are also three specimens of *L. fruticosus* Buek, but only one of these is labelled *Echium fruticosum*. One of the others bears the inscription *E. scabrum*, and this is the only specimen so named by Thunberg. One may therefore conclude that this plant is the one to which he refers in his

'Flora Capensis' as *E. scabrum*. On Buek's authority, the specimen of *E. scabrum* in Lehmann's Herbarium is *Lobostemon fruticosus* Buek. Thus we see that both Thunberg and Lehmann had the same plant in mind as *Echium scabrum*, that plant being *Lobostemon fruticosus* Buek. De Candolle, however, established *Lobostemon scaber* as the equivalent of *L. Thunbergianus* Buek, which is synonymous with *L. trigonus* Buek! C. H. Wright, in the 'Flora Capensis' followed de Candolle.

Note 2.—Certain forms of *L. fruticosus* Buek collected by Dr. John Muir in the Riversdale and Mossel Bay Districts are much less hairy than is usual in this species. Muir 1453 from Cloete's Pass, Mossel Bay, shows on the same sheet a plant which apart from the reduced number of hairs on the leaves agrees with *L. fruticosus*, and a second plant with rather more concave leaves and more congested cymes. This latter plant agrees with *Muir* 4172 from Derde River, Riversdale, and *Muir* 1761 from Albertinia. Whether these plants are forms of *L. fruticosus* Buek or whether they are the result of hybridisation, I am not prepared to say.

17. LOBOSTEMON CURVIFOLIUS Buek in Linnaea, xi, p. 137 ; DC. Prod. x, p. 9 ; C. H. Wright in Fl. Cap. iv, 2, p. 39. *L. magnisepalum* N. E. Br. in Journ. Linn. Soc. xlv, p. 141. *Echium argenteum* Linn. Mant. ii, p. 202, not of Bergius. *E. fruticosum* Linn. MS. no. 145 conf. Proc. Linn. Soc. 1917–1918, Suppl. p. 10. *E. curvifolium* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

An undershrub, moderately branched ; usually between 30 and 60 cm. high. *Branches* villous when young, but becoming less hairy with age. *Leaves* linear or linear-lanceolate, acute or obtuse, often recurved at the apex, from 1 to 4·5 cm. long and 2 to 6 mm. wide ; leaves increasing in size between the first and second seasons ; both surfaces covered with hairs ; when young these are soft, adpressed, and silvery, but when older they develop bulbous bases and stand out from the leaf-surface. *Inflorescence* cymose, cymes somewhat short when young, but elongating with age. *Bracts* similar to the leaves, but smaller. *Calyx* a little more than half as long as the corolla or less ; sepals linear to linear-lanceolate, acute, equal or nearly so, softly hairy with adpressed hairs. *Corolla* funnel-shaped ; tube widening gradually, obliquely zygomorphic, up to 2·5 cm. long, shortly pubescent outside, blue or pink. *Staminal scales* inserted about one-fifth of the way up the tube, reduced to small transverse ridges. *Stamens* of three lengths, included or just exserted, adnate to the corolla for a short distance above the insertion of the scales. *Style* hairy. Each *nutlet* with three, faintly developed, longitudinal ridges, rugose-tuberculate over the whole surface.

Habitat. Sandy places ; lower mountain slopes.

Flowering season. September to October.

CALEDON : *Ecklon and Zeyher* ! *Bolus* ! *Kuntze* ! *Marloth* 7084 ! *Rogers* 28916 ! between Genadendal and Donker Hoek, *Burchell* 7917 ! Houw Hoek, *Levyns* 2290 ! *Levyns* 3468 ! *Penther* 1816 ! *Penther* 1821 ! between Bot River and Zwart-

berg, *Ecklon* 55 ! Zwartberg, *Galpin* 4346 ! SWELLENDAM : Grootvadersbosch, *Mundt* ! RIVERSDALE : Elandskop, Albertinia, *Muir* 1761 ! WITHOUT LOCALITY : *Breutel* ! *Burmann* ! *Lichtenstein* 175 !

Note on the Linnaean specimen ' 145 argenteum ' described by
N. E. Brown as Lobostemon magnisepalum.

I have seen this specimen, and am of the opinion that it is a form of *L. curvifolius* Buek. Like many other species in this genus, *L. curvifolius* shows great variability in leaf-size and hairiness. The Linnaean specimen in these respects is intermediate between plants gathered by Penther and myself at Houw Hoek and Muir 1761 from the Riversdale district. Apart from a slight difference in leaf-size there is no character by which it can be separated from *L. curvifolius* Buek.

I suspect that ' montibus nigris ' of Linné is the Zwartberg of Caledon, a locality in which this species has been collected.

18. LOBOSTEMON LUCIDUS Buek in Linnaea, xi, p. 136 ; DC. Prod. x, p. 10 ; C. H. Wright in Fl. Cap. iv, 2, p. 43. *Echium lucidum* Lehm. in Linnaea, v, p. 374.

An undershrub about 20 cm. in height, hardly branching above ground-level, only becoming woody towards the base, which is covered by the remains of old leaves. *Branches* villous. *Leaves* crowded, acute, linear or linear-oblanceolate, 2 to 4·5 cm. long and 2·5 to 6 mm. wide, weakly villous when young, sparsely hairy or nearly glabrous and shining when old. *Inflorescence* of several rather loose cymes, all the axes villous. *Bracts* much less strongly developed than usual in the genus, not concealing the calyx, linear, villous. *Calyx* about half the length of the corolla ; sepals linear, densely villous. *Corolla* funnel-shaped ; tube widening gradually, very slightly oblique or regular, up to 2·5 cm. long, shortly hairy outside, pink or blue. *Staminal scales* reduced to small transverse ridges, inserted about one-fifth of the way up the tube. *Stamens* of three lengths or sometimes all dissimilar in length, adnate to the corolla above the insertion of the scales. *Style* hairy. *Nutlets* not seen.

Habitat. Sandy places ; lower hill-slopes.

Flowering season. August to October.

BREDASDORP : *Levyns* 2393 ! *Levyns* 2573 ! SWELLENDAM : *Ecklon and Zeyher* ! RIVERSDALE : ' *Herb. Schlechter* ' ! WITHOUT LOCALITY : *Beil and Mund.*

Note.—Buek states that this species was founded on an imperfect specimen from ' Grootvadersbosch ' collected by Beil and Mund in 1825. A specimen collected by Ecklon and Zeyher, no. 91 (now in Berlin), is stated by Drège (Linnaea, xx, p. 258) to be the same plant as that of Mund. I have seen Ecklon and Zeyher's specimen, which was collected in November, obviously very late in its flowering season, as most of the flowers were dead. The leaves answer Lehmann's description well. There is a second specimen in Berlin among Schlechter's plants, with ' Riversdale 1893 ' inscribed in MacOwan's writing.

This specimen is in better condition, and shows that whereas the old leaves are almost glabrous and similar to those of Ecklon and Zeyher 91, the young leaves have long scattered hairs. This Riversdale plant forms a connecting-link with specimens from Bredasdorp (Levyns 2573 and Levyns 2393), where the leaves are more hairy than in the other specimens. This species, however, is so well defined in habit and floristic features that I have no hesitation in placing all these specimens together under one species.

19. LOBOSTEMON STRIGOSUS Buek in Linnaea, xi, p. 136 ; DC. Prod. x, p. 9 ; C. H. Wright in Fl. Cap. iv, 2, p. 31. *Echium strigosum* Lehm. Pl. Asper. p. 432 (1818) ; Lehm. Ic. t. xvii (1821) ; Thunb. Fl. Cap. ed. Schult. p. 164 (1823).

A branched spreading shrub about 60 cm. in height. *Branches* hispid with fine and coarse hairs mixed. *Leaves* linear, linear-oblong, or linear-lanceolate, obtuse or occasionally acute and slightly recurved, 2 to 7 cm. long, 3 to 10 mm. wide, coarsely hispid, especially on the lower surface, very harsh to the touch. *Inflorescence* cymose, consisting of several markedly unilateral branches never very crowded. *Bracts* similar to the leaves, but lanceolate or ovate. *Calyx* rather more than half as long as the corolla ; sepals linear, hispid, some-times one shorter than the rest. *Corolla* funnel-shaped ; tube widening gradually ; obliquely zygomorphic or with two lobes slightly larger than the rest, 2 cm. in length or less, pubescent outside ; colour usually a deep bright blue. *Staminal scales* inserted about a quarter of the distance up the tube or higher, reduced to transverse ridges. *Stamens* of three lengths, the longest usually slightly exserted, adnate to the corolla above the insertion of the scales. *Style* hairy. Each *nutlet* with one median and two lateral ridges, roughly rugose-tuberculate : tubercles strongly developed on the ridges.

Habitat. Usually on fine-grained soils ; a constituent of rhenosterveld.

Flowering season. August to October.

CALEDON : Bot River, *Schlechter* 9437 ! *Levyns* 2277 ! near Caledon, *Levyns* 2275 ! SWELLENDAM : *Zeyher* ! *Drège* ! *Pappe* ! Buffelsjagt ! ? *Zeyher* 3453 ! RIVERSDALE : Albertinia, *Muir* 4789 ! MOSSEL BAY : *Alexander* ! *Rogers* 4177 ! *Drège* 7847, from Trado, may be a hybrid between this and some other species.

Note.—Lehmann's figure fits this species well. In Thunberg's Herbarium I have seen no specimen belonging to it, though there are two plants named *Echium strigosum.* One is *Lobostemon glaucophyllus* Buek. The other is one of the modifications of *L. trichotomus* DC., which I believe to be of hybrid nature. However, Thunberg's description in his 'Flora Capensis' would apply to *L. strigosus* Buek, and the fact that there is no specimen of this species among Thunberg's plants does not preclude the possibility that Thunberg may have seen a specimen of that plant. I have therefore retained Thunberg's reference for this species.

20. LOBOSTEMON TRIGONUS Buek in Linnaea, xi, p. 135 ; DC. Prod. x, p. 9 ; C. H. Wright in Fl. Cap. iv, 2, p. 32. *L. Thunbergianus* Buek in Linnaea, xi, p. 135, *L. obtusifolius* DC. Prod. x, p. 7 ; C. H. Wright in Fl. Cap. iv, 2, p. 32,

L. scaber DC. Prod. x, p. 6 ; C. H. Wright in Fl. Cap. iv, 2, p. 34. *Echium trigonum* Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. i, 2, p. 784 (1798) ; Pers. Syn. Pl. i, p. 163 (1805) ; Thunb. in Schrad. n. Journ. i, 3, p. 42 (1806) ; Lehm. Pl. Asper. p. 482 (1818) ; Lehm. Ic. t. xxxvi (1821) ; Thunb. Fl. Cap. ed. Schult. p. 166 (1823). *E. obtusifolium* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A branched shrub about 60 cm. high. *Branches* villous with fine and moderately coarse hairs mixed. *Leaves* oblong or oblong-lanceolate, obtuse, with an average length of 2 cm. and an average width of 8 mm., both surfaces with rather stiff bulbous-based hairs, which sometimes are adpressed, but more usually stand out from the surface ; in some cases the leaf becoming almost glabrous and white-punctate with age. *Inflorescence* cymose, cymes rather condensed when young, but elongating with age. *Bracts* similar to the leaves, but smaller ; ovate or lanceolate. *Calyx* half as long as the corolla or longer ; sepals equal or subequal, linear, hispid on the outer surface, sometimes with the hairs adpressed. *Corolla* funnel-shaped ; tube widening gradually, slightly oblique and zygomorphic, 2 cm. long or less, pubescent outside, usually blue. *Staminal scales* inserted about one-quarter of the way up the corolla-tube, reduced to transverse ridges. *Stamens* of three lengths, all usually included, adnate to the corolla for a short distance above the insertion of the scales. *Style* hairy. Each *nutlet* with a median and two or four lateral ridges, rugose-tuberculate, the tubercles being most strongly developed on the lateral ridges.

Habitat. There are few records of the habitat. Fine-grained soils ; but possibly on other types of soil as well.

Flowering season. August to October.

BREDASDORP : *Bolus* 20001 ! MOSSEL BAY, ? *Burchell* 6301 ! KNYSNA : Plettenberg Bay, *Rogers* 29260 ! HUMANSDORP : *Galpin* 4344 ! *Rogers* 2906 ! UITENHAGE : *Zeyher* 976 ! *Ecklon and Zeyher* ! *Penther* 1827 ! Zuurberg, *Ecklon and Zeyher* ! Zwartkops River, *Drège* 7850 ! *Zeyher* 283 ! Coega, *Rogers* 2109 ! between Coega River and Sunday's River, *Drège* 7851 ! near Lourie, *Penther* 1825 ! ' Aloes ', *D. L. Drège* 3136 ! PORT ELIZABETH : *Holub* ! *Zeyher* 78 ! *West* 114 ! *Laidley* ! *Rosenbrock* 309 ! *Hoffmann* 58 ! *Tyson* 2281 ! *Bolus* 9125 ! Algoa Bay, *Forbes* 81 ! Van Stadensberg, *Zeyher* 1242 ! Grasrug, *Baur* 1022 ! Bethelsdorp, *Zeyher* ! Baakens Valley, *Cruden* 397 ! ALEXANDRIA : between Rautenbach's and Addo Drifts, *Burchell* 4210 ! Kenkelbos Station, *Muir* 4712 ! WITHOUT LOCALITY : *Thunberg* ! *Thom* ! *Verreaux* !

21. LOBOSTEMON COLLINUS Schlechter ex C. H. Wright in Fl. Cap. iv, 2, p. 28. *Echium Schlechteri* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A branched shrub. *Branches* with long scattered hairs when young, becoming glabrous later. *Leaves* erect, oblong, obtuse, up to 3·5 cm. long and 5 mm. wide, scantily ciliate, and with a few hairs on both surfaces when young,

becoming glabrous with age, though marked with the permanent bases of the hairs. *Inflorescence* cymose, cymes closely arranged. *Bracts* similar to the leaves, somewhat ovate in the upper part of each cyme. *Calyx* about three-quarters of the length of the corolla or more ; sepals equal or nearly so, oblong, obtuse, with a pronounced central vein, with scattered adpressed hairs, especially towards the base ; apex sometimes almost glabrous. *Corolla* funnel-shaped ; tube widening gradually, somewhat oblique, about 1 cm. in length, scantily pubescent outside, the pubescence being most marked on the central vein of each lobe. *Staminal scales* near the base of the tube, ridge-like. *Stamens* of three lengths, adnate to the corolla-tube above the scales ; longest stamens just exserted. *Nutlets* not seen.

Habitat. Sandy places.

BREDASDORP : Vogel Vlei, *Schlechter* 10483 !

22. LOBOSTEMON OEDERIAEFOLIUS DC. Prod. x, p. 7 ; C. H. Wright in Fl. Cap. iv, 2, p. 33. *Echium oederiaefolium* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A moderately branched shrub about 1 m. high. *Branches* covered with hairs of varying sizes, some hairs rather long. *Leaves* linear to linear-lanceolate, acute, from 2 to 3·5 cm. in length and from 3 to 6 mm. in width ; midrib the only nerve well defined ; covered with scattered bulbous-based hairs on both surfaces, the coarsest hairs being found on the under side towards the apex. *Inflorescence* cymose ; flowers rather crowded when young ; axis elongating with age. *Bracts* similar to the leaves, but more definitely lanceolate. *Calyx* about half as long as the corolla or shorter ; sepals lanceolate, somewhat unequal, the anterior sepal usually smaller than the rest, two or three of the sepals occasionally joined for some distance from the base, glabrous outside except for stiff hairs along the margin and a few on the well-marked central vein. *Corolla* up to 4 cm. long, funnel-shaped, tube widening gradually, oblique, lobes often crinkled along the margin, slightly hairy outside ; blue or pink. *Staminal scales* inserted about one-fifth of the way up the tube, reduced to very small transverse ridges. *Stamens* of three lengths ; all more or less included, adnate to the corolla for some distance above the insertion of the scales. *Style* hairy. Each *nutlet* with three well-defined longitudinal ridges and covered with rather prominent tubercles.

Habitat. Sandy soils : lower mountain slopes.

Flowering season. September to October.

CERES : Mitchell's Pass, *Kolbe*, 14381 in Herb. Bolus ! Matroosberg, *Phillips* 2047 ! WORCESTER : *Stokoe* 1247 ! De Doorns, *Marloth* 1973 ! Bokke River, *Levyns* 941 ! Eendragt, *Levyns* 325 ! ROBERTSON : Cogman's Kloof, *Levyns* 49 ! Robertson, *Levyns* 2774 ! WITHOUT LOCALITY : *Drège* 9358 !.

23. LOBOSTEMON MUIRII Levyns, sp. n. ; caule ramosissimo ; foliis linearibus acutis glabriusculis viridibus pallidis ; cymis confertis ; calycis lobis sub-aequalibus corolla parum brevioribus ; corolla magna infundibuliformi lutea

pallida nervis rubris extus puberula ; squamis parvis orbiculatis ; staminibus inaequalibus fere inclusis.

A much-branched shrub about 1 m. high. *Branches* when young purplish brown, covered with white adpressed hairs. *Leaves* linear, acute, with the midrib well defined, other veins obscure, 2·5 to 7 cm. long, 3 to 5 mm. broad, pale green, with small scattered adpressed hairs, which render the surface rough to the touch, almost glabrous in appearance. *Inflorescence* cymose, with cymes rather crowded at the tips of the branches, usually over-topped by the enveloping leaves. *Bracts* similar to the leaves, but linear-lanceolate in shape. *Calyx* about as long as the corolla-tube ; sepals linear, acute, somewhat unequal in size, glabrous or with a few scattered adpressed hairs. *Corolla* funnel-shaped ; tube widening gradually, slightly oblique and zygomorphic, about 2 cm. in length, glabrous outside, when young greenish cream colour with red veins, flushed with brownish red inside, changing to a light brown in older flowers. *Staminal scales* inserted near the base of the tube, rounded and ridge-like. *Stamens* of three lengths ; the longest pair usually just exserted, adnate to the corolla for a short distance above the insertion of the scales. *Style* shortly hairy. Each *nutlet* with three fairly well-marked longitudinal ridges, tuberculate, especially on the two lateral ridges.

Habitat. Sandy ground ; lower mountain slopes.

Flowering season. July. The flowering season appears to be a very short one.

RIVERSDALE : Muiskraal, *Muir* 3638 ! *Levyns* 2110 ! *Levyns* 2111 ! Waterval, *Muir* 2812 ! *Muir* 3010.

24. LOBOSTEMON DECORUS Levyns, sp. n. ; caule ramoso ; foliis linearibus acutis glabriusculis viridibus ; calycis lobis aequalibus aut subaequalibus pilosiusculis corolla fere dimidio brevioribus ; corolla magna infundibuliformi extus puberula coerulea ; squamis parvis ; staminibus inclusis inaequalibus.

A moderately branched shrub, rather under 1 m. in height. *Branches* with short scattered hairs when young, becoming almost glabrous with age. *Leaves* linear, acute, with the midrib distinct, but the other veins obscure, from 2 to 7 cm. long and from 2·5 to 7 mm. wide, deep, true green in colour, with short scattered bulbous-based hairs along the margin and a few on both surfaces towards the apex when young ; hairs falling off early and leaving the bases only ; general appearance of the leaf glabrous. *Inflorescence* cymose, cymes somewhat crowded when young, but elongating slightly with age. *Bracts* similar to the leaves, but linear-lanceolate and oblique. *Calyx* from one-third to three-quarters the length of the corolla ; sepals linear, acute, slightly dissimilar or equal, with scattered adpressed hairs on the outer surface and along the margin. *Corolla* funnel-shaped ; tube widening gradually, somewhat obliquely zygomorphic, 2·5 cm. in length or less, with minute hairs outside in the upper portion ; usually bright blue, with deep pink markings. *Staminal scales* inserted about one-fifth of the way up the corolla-tube, rather small and ridge-like. *Stamens* of three lengths, the longest about the length

of the corolla, adnate to the corolla for a short distance above the insertion of the scales. *Style* hairy. Each *nutlet* bluntly ovoid, with the median ridge prominent only at the apex, and the lateral ridges obscure, very finely rugose.

Habitat. Sandy mountain slopes, 2,000 to 4,500 feet.

Flowering season. September to November. At altitudes about 2,000 feet the flowering season appears to be a short one in September, but the only collection at a fairly high altitude (4,500 feet) was made in November.

LADISMITH : *Levyns* 2094 ! *Levyns* 2321 ! *Levyns* 2413 ! Seven Weeks' Poort, *Levyns* 2462 ! Roodeberg, *Compton* 3905 !

25. LOBOSTEMON MARLOTHII Levyns, sp. n. ; ramis simplicibus erectis ; foliis oblongo-lanceolatis aut oblongis acutiusculis aut obtusis strigosis ; calycis lobis subaequalibus hispidis corolla fere dimidio brevioribus ; corolla magna infundibuliformi extus puberula saepe coerulea ; squamis parvis ; staminibus inaequalibus inclusis aut paulum exsertis.

A shrub, usually sparsely branched and with an erect habit. *Branches* densely hairy with rather long hairs. *Leaves* usually crowded towards the ends of the branches and imbricate, oblong or oblong-lanceolate, acute or obtuse, 1·5 to 4 cm. long (usual length about 2 cm.) and 3 to 5 mm. wide, densely strigose on both surfaces, hairs being rather coarser towards the apex, harsh to the touch. *Inflorescence* cymose, with the cymes crowded when young. *Bracts* similar to the leaves, but becoming proportionally wider as they diminish in size. *Calyx* less than half the length of the corolla ; one sepal usually smaller than the rest ; sepals linear, acute, coarsely strigose and ciliate with stiff bristles. *Corolla* up to 2·2 cm. long, funnel-shaped, tube widening gradually, obliquely zygomorphic, minutely pubescent outside ; usually blue. *Staminal scales* inserted about a quarter of the way up the tube, rather small and ridge-like. *Stamens* of three lengths, the two longest included or just exserted, adnate to the corolla for some distance above the insertion of the scales. *Style* hairy. Each *nutlet* with three not very pronounced longitudinal ridges, more or less uniformly covered with tubercles, occasionally with larger tubercles on the lateral ridges.

Habitat. Sandy mountain slopes, at an altitude of 3,500 feet and upwards.

Flowering season. August to October.

WORCESTER : Matjesfontein, *Marloth*, 2942 ! *Compton* 3288 ! *Compton* 2646 ! *Compton* 3289 ! Whitehill, *Compton* 3193 ! Tweedside, *Levyns* 2370 ! Witteberg, Matjesfontein, *Thoday* 17291 in Herb. Bolus ! LADISMITH : *Marloth* 2942 ! Seven Weeks' Poort, *Phillips* 1556 ! *Phillips* 1558 ! OUDTSHOORN : *Tyson*, 14343 in Herb. Bolus ! Zwartberg Pass, *Bolus* 11608 ! *Tyson* 14342 ! WILLOW-MORE : Modderfontein, *Andreae* 1046 !

26. LOBOSTEMON MONTANUS Buek in Linnaea, xi, p. 132 ; C. H. Wright in Fl. Cap. iv, 2, p. 30 (excluding var. *minor* C. H. Wright) ; *Echium montanum* DC. Prod. x, p. 15,

A much-branched shrub, about 1 m. high, but varying largely with the habitat; occasionally in sheltered ravines reaching nearly 2 m. in height, the main axis sometimes being about 8 cm. in diameter. *Branches* densely covered with rather long white hairs. *Leaves* acute or obtuse, oblanceolate, with the midrib projecting on the lower surface, ranging in size from 4 to 20 cm. in length and 1 to 5 cm. in width, both surfaces covered with hairs. *Inflorescence* consisting of several rather loosely packed cymes, which do not elongate greatly in the fruiting stage. *Bracts* similar to the leaves, but smaller. *Calyx* almost as long as the corolla-tube ; sepals linear, acute, slightly unequal in size, hairy. *Corolla* tubular, not widening greatly, and with somewhat small oblong lobes, regular or nearly so, rarely exceeding 2 cm. in length, hairy outside, pale blue. *Staminal scales* inserted close to the base of the tube, small and ridge-like. *Stamens* equal in length or nearly so, just included or exserted, adnate to the corolla-tube for some distance above the insertion of the scales. *Style* hairy. Each *nutlet* with three obscure longitudinal ridges and poorly developed tubercles.

Habitat. Sandy places, both exposed and sheltered.

Flowering season. July to September.

CAPE : Table Mountain, *Pappe* ! *Bolus* 7237 ! ' Stinkwater ', *Rehmann* 1214 ! Woody Ravine, *Levyns* 2397 ! Devil's Peak, *Drège* ! *Bolus* 3947 ! *Burchell* 8474 ! *Levyns* 2879 ! *Wilms* 3462 (partly) ! *Pappe* ! *Marloth* 1797 ! Muizenberg, *Zeyher* 3450 ! *Pappe* ! *Gamble* 22126 ! *MacOwan* 922 ! *Krauss* ! *Pearson* 232 ! *Galpin* 10346 ! *Flanagan* 2476 ! Kalk Bay, *Alexander* ! *Levyns* 2398 ! *Levyns* 2578 ! Fish Hoek *Bolus* ! between Fish Hoek and Simonstown, *Hutchinson* 89 ! Simonstown, *Jameson* ! between Millers' Point and Smitswinkel Bay, *Phillips* ! Smitswinkel Bay, *Salter* 302 ! Cape Point, *Rogers* 29253 ! above Tokai Plantation, *Wolley Dod* 1274 (or 1276) ! Newlands, *Marloth* 7003 ! above Groote Schuur, *Wolley Dod* 3360 ! STELLENBOSCH : near Sir Lowry's Pass, *Burchell* 8294 ! CALEDON : Onrust, *Zeyher* 3448 ! WITHOUT LOCALITY : *Burmann* ! *Thunberg* (the left-hand specimen on a sheet labelled *Echium fruticosum*) ! *Banks* ! *Sparrman* ! *Verreaux* ! *Sieber* 38 ! *Forbes* ! *Drège* 375 ! *Boivin* 690 ! *MacWilliam* ! *Scholl* 318 ! *Nelson* !

Note.—L. *Sprengelianus* Buek is almost certainly this species, but I have not seen the specimen quoted by Buek.

27. LOBOSTEMON GRANDIFLORUS Levyns, comb. nov. *Lobostemon formosus* Buek in Linnaea, xi, p. 132. *Echium grandiflorum* Andr. Bot. Rep. t. xx (1797) ; Vent. Jard. Mal. t. xcvii (1803) ; Desf. Arb. i, p. 177, not Fl. Atlant. (1809) ; Bot. Reg. t. cxxiv. (1816). *E. formosum* Pers. Syn. Pl. i, p. 163 (1805) ; Lehm. Pl. Asper. p. 418 (1818) ; DC. Prod. x, p. 15 (1846) ; C. H. Wright in Fl. Cap. iv, 2, p. 44 (1904). *E. longiflorum* Dum. Cours. Bot. Cult. ed. 2, Suppl. 7, p. 147. *E. regulariflorum* Ker-Gawl. Recens. ii, n. 42 (1801). *E. tubiferum* Poir. Encycl. viii, p. 663 (1808).

A branched shrub, usually about 1 m. high, sometimes reaching nearly 2 m.

in height. *Branches* almost glabrous, but for a few prickle-like hairs. *Leaves* linear or linear-lanceolate, somewhat acuminate, with a prominent midrib on the lower surface, reaching 13 cm. in length and 1·7 cm. in width, upper surface and margin scabrid with bulbous-based hairs, lower surface almost glabrous. *Inflorescence* of several closely arranged cymes. *Bracts* similar to the leaves, upper ones smaller and lanceolate. *Calyx* rather variable in size, but usually at least two-thirds the length of the corolla ; sepals unequal in size, the two anterior sepals, and occasionally one of the lateral as well, joined for more than half their length ; veins distinct ; spinose-ciliate, with a few similar spines towards the base of the larger veins, otherwise glabrous outside. *Corolla* tubular, not widening greatly, and with rather small lobes, regular, usually between 4 and 5 cm. long, outer surface with very short scattered hairs ; brilliant red. *Staminal scales* situated about one-fifth of the way up the corolla-tube, much reduced, represented by bulbous swellings covered with stiff hairs, which extend upwards on to the bases of the adnate filaments. *Stamens* equal or nearly so, just included or slightly exserted, adnate to the corolla-tube for some distance above the swellings. *Style* hairy. *Fruit* not seen.

Habitat. Mountain slopes ; in ravines.

Flowering season. September to November.

PAARL : French Hoek, *Schlechter* 9284 ! *Marloth* 7518 ! Banhoek, *Marloth* 13771 ! STELLENBOSCH : Hottentot's Holland, *Prior* ! Knor Hoek, Sir Lowry's Pass, *Marloth* ! WITHOUT LOCALITY : *Gay* ! *Rogers* !

Note.—A specimen (without locality) collected by Rogers in 1880 has much narrower leaves with revolute margins, and all parts more hairy than usual. In view of the fact that all these features are subject to variation in this genus, I have not established a separate species for this plant.

28. LOBOSTEMON SANGUINEUS Schlechter in Engl. Bot. Jahrb. xxiv, p. 450 ; C. H. Wright in Fl. Cap. iv,·2, p. 27. *Echium sanguineum* I. M. Johnston in Contrib. Gray Herb. n.s. lxxiii, p. 52 (1924).

A robust shrub, 1 to 1·5 m. in height, moderately branched. *Branches* densely papillose-scabrid, very leafy. *Leaves* erecto-patent, ovate, acute, denticulate-scabrid on the margins and under surface of the midrib, and also sometimes near the apex on the under surface, glabrous elsewhere, coriaceous ; up to 6 cm. in length and 2 cm. wide ; leaves a true green. *Inflorescence* cymose, dense, and regularly disposed. *Bracts* similar to the leaves, but smaller and relatively wider, overtopping the flowers. *Calyx* two-thirds the length of the corolla or more ; sepals free to the base, very unequal in size, coriaceous, the largest leaf-like and similar to the bract, becoming progressively less leaf-like with diminution in size ; margin ciliate with stiff bristles, similar bristles being found on the nerve. *Corolla* up to about 3 cm. long, tubular, not widening greatly ; lobes obtuse with an undulating margin, regular, hairy outside in the upper portion and inside as far as the separation of the lobes ; colour red. *Staminal scales* situated about one-quarter of the way up the tube, small, rounded, and ridge-like, densely hairy everywhere excepting the upper surface,

Stamens equal or with one shorter than the rest, adnate to the corolla for some distance above the insertion of the scales. *Style* hairy (the disc below the ovary is more prominent than in other species). Each *nutlet* without any longitudinal ridges, rather smooth, though faintly tuberculate in the lower portion, inner faces more tuberculate than the rest of the surface.

Habitat. Sandy soil; sheltered slopes of valleys on low hills.

Flowering season. February to April.

BREDASDORP : Elim, *Schlechter* 7683 ! Bredasdorp, *Levyns* 2394 ! *Levyns* 3089 !

ECHIOSTACHYS Levyns, gen. nov.

Genus *Lobostemoni* valde affine, sed differt herbae perennes, foliis radicalibus, cymis multis parvifloris in spicas dispositis, calycibus et pedicellis demum accrescentibus, et squamis ad basin filamentorum nullis.

Flowers bisexual, 5-merous. *Sepals* free or nearly so, equal, linear or spathulate, accrescent. *Corolla* narrowly funnel-shaped, with obtuse lobes, regular. *Stamens* equal or subequal, epipetalous, exserted; filaments with hairs at or near the base, the hairs sometimes tufted; anthers subglobose or oblong; obtuse. *Ovary* 4-lobed on a flat or slightly convex disc; style gynobasic, simple, with a small, hardly bifid stigma. *Fruit* of four nutlets, surface rugose-tuberculate or almost smooth.

Perennial herbs with somewhat woody underground stems, giving off tufts of leaves and flowering shoots annually; the inflorescence and usually all other aerial parts hairy. *Inflorescence* a dense pseudo-spike, occasionally interrupted at the base, composed of numerous short cymose branches, densely arranged around a stout central axis which rarely branches; cymules elongating somewhat in the fruiting stage. *Flowers* white, cream, purple, or red.

An endemic South African genus. Species 3.

Note.—Throughout the genus the pedicels and calyx show a considerable increase in size (particularly length) after anthesis. The corolla does not fall off at once, and in dried specimens much confusion has been caused by these pecularities, resulting in the same plant receiving different names at different stages of development. For instance, Lehmann (Ic. t. i and xxxiii) gives excellent representations of young and old states of the inflorescence of *Echiostachys incanus*. The young stage is named *Echium spicatum* L. f., and the older stage, *E. incanum* Thunb.

Key to the Species.

A. Leaves narrow-linear, much attenuated at the apex; hairs at
the base of the stamens tufted .... 1. *incanus.*

AA. Leaves oblanceolate or elliptic; not or hardly attenuated at
the apex; hairs not aggregated at the base, but spread over
the adnate portion of the filament.

B. Corolla usually more than 1 cm. in length, white; fruit
rugose-tuberculate .... 2. *spicatus.*

BB. Corolla less than 1 cm. in length; purple or red; fruit
almost smooth .... 3. *Ecklonianus.*

1. ECHIOSTACHYS INCANUS Levyns, comb. nov. *Lobostemon spicatus* Buek in Linnaea, xi, p. 145 (1837); C. H. Wright in Fl. Cap. iv, 2, p. 41 (1904). *L. splendens* Buek in Linnaea, xi, p. 146; C. H. Wright in Fl. Cap. iv, 2, p. 40. *Echium spicatum* Linn. f. Supp. p. 132 (1781); Lam. Ill. p. 413, no. 1861 (1791); Thunb. Prod. p. 33 (1794); Willd. Sp. Pl. i, 2, p. 786 (1798); Pers. Syn. Pl. p. 163 (1805); Thunb. in Schrad. n. Journ. i, 3, p. 41 (1806); Lehm. Pl. Asper. p. 435 (1818); Lehm. Ic. t. 1 (1821); Thunb. Fl. Cap. ed. Schult. p. 165 (1823); DC. Prod. x, p. 14 (1846). *Echium incanum* Thunb. Prod. p. 33 (1794); Willd. Sp. Pl. i, 2, p. 786 (1798); ·Pers. Syn. Pl. i, p. 163 (1805); Thunb. in Schrad. n. Journ. i, 3, p. 39 (1806); Lehm. Pl. Asper. p. 436 (1818); Lehm. Ic. t. xxxiii (1821); Thunb. Fl. Cap. ed. Schult. p. 164 (1826). *E. splendens* DC. Prod. x, p. 15.

A perennial herb with a thick, somewhat woody underground stem, which gives off tufts of leaves and flowering shoots annually, 40 cm. high in vigorous specimens, but usually less; flowering shoot covered with rather weak hairs. Basal leaves linear, attenuated at both ends, acute, up to 22 cm. in length and 15 mm. in width, but usually smaller, with rather long·scattered hairs on both surfaces; leaves on the flowering axis smaller than the basal ones and lanceolate near the flowers. Flowering portion of the inflorescence from 2·5 to 15 cm. long and from 2·5 to 3 cm. wide, flowers shortly pedicelled. *Bracts* rather small, subtending each cymule. *Calyx* about half to three-quarters as long as the corolla; sepals linear-oblong, obtuse, densely covered with upwardly directed hairs, almost doubling its length in the fruiting stage, and with hairs standing out from the surface. *Corolla* with a narrow cylindrical basal portion, widening gradually in the upper part, about 6 mm. long, hairy along the central vein of each lobe; white or cream colour, faintly scented. *Stamens* subequal, often one rather shorter than the rest, exserted, arising about one-third or one-half of the way up the corolla-tube, with a tuft of hairs at the point of insertion, hardly adnate. *Style* with spreading hairs in the lower portion. Each *nutlet* with a median ridge, the whole surface rugose-tuberculate, with short, stiff, glassy hairs arising from the larger tubercles.

Habitat. Sandy places at low elevations.

Flowering season. August to October.

CLANWILLIAM: Brakfontein, *Ecklon and Zeyher* 76! PIQUETBERG: *Diels* 162! Goedverwacht, *Bolus* 13613! CAPE: Koeberg, *Zeyher* 2484! PAARL: *Drège* 7855! Uitkyk, *MacOwan* 2484: between Durbanville and Wellington, *Levyns* 2525! STELLENBOSCH: *Duthie* 676! *Sanderson*! Somerset West, *Grey*! *Alexander*! *v. Ludwig*! Van der Stel, *Smith* 3226! Eerste River, *Bolus* 9945! Faure, *Levyns* 2545! Gordon's Bay, *Levyns* 3210! CALEDON: River Zonde Einde, *Lichtenstein* 174! WORCESTER: Hex River Valley, *Marloth* 6193! BREDASDORP: Elim, *MacOwan*! SWELLENDAM: *Mundt*! *Ecklon and Zeyher*! WITHOUT LOCALITY: *Thunberg*! *Niven* 21! *Forsyth*! *Forbes* 132 (Algoa Bay is the locality given, but it is almost certainly wrong). *Muir* 3920!

Note on Lobostemon viridi-argenteus *Buek.*

I have refrained from quoting this species, as it is probably only a form of *Echiostachys incanus.* It is based on a specimen collected by Ecklon, quoted by Buek as having come from 'Piquet-berge (Stellenbosch)'. The only specimen I have seen is that of Ecklon and Zeyher 77, which is imperfect. Apart from its more silvery appearance, it does not differ from *Echiostachys incanus.* In this genus, as in *Lobostemon,* the degree and type of hairiness on the vegetative parts are most variable characters, and quite unsuited for establishing separate species in the absence of any other diagnostic features.

2. ECHIOSTACHYS SPICATUS Levyns, comb. nov. *Lobostemon caudatus* Buek in Linnaea, xi, p. 145 ; C. H. Wright in Fl. Cap. iv, 2, p. 40. *L. eriostachyus* Buek in Linnaea, xi, p. 148 ; C. H. Wright in Fl. Cap. iv, 2, p. 40. *L. latifolius* Buek in Linnaea, xi, p. 147 ; C. H. Wright in Fl. Cap. iv, 2, p. 39. *L. alope-curoideus* C. H. Wright in Fl. Cap. iv, 2, p. 39. *Echium spicatum* Burm. f. Prod. Cap. p. 4 (1768). *Echium caudatum* Thunb. Prod. p. 33 (1794) ; Willd. Sp. Pl. i, 2, p. 786 (1798) ; Pers. Syn. Pl. i, p. 164 (1805) ; Thunb. in Schrad. n. Journ. i, 3, p. 43 (1806) ; Lehm. Pl. Asper. p. 434 (1818) ; Lehm. Ic. t. xxxii (1821) ; Thunb. Fl. Cap. ed. Schult. p. 165 (1823) ; DC. Prod. x, p. 13 (1846). *E. eriostachyum* DC. Prod. x, p. 14. *E. latifolium* DC. Prod. x, p. 14. *E. alope-curoideum* DC. Prod. x, p. 15.

A perennial herb with a somewhat woody underground stem, which gives off tufts of leaves and flowering shoots annually, 40 cm. in height in large specimens, but usually less ; flowering shoot beset with long soft hairs or occasionally almost glabrous, especially near the base. Basal *leaves* oblanceolate or elliptic, much attenuated at the lower end, somewhat dilated and ciliate at the extreme base, obtuse or somewhat acute, variable in size, with an average of 20 cm. in length and 3 cm. in width, in vigorous shade-forms reaching 45 cm. in length and 5 cm. in width, usually with weak scattered hairs on both surfaces, occasionally with the upper surface glabrous ; leaves on the flowering shoot smaller than the basal ones and becoming lanceolate near the flowers, but with the same type of indument as the basal leaves. *Inflorescence* variable in size, ranging from 17 cm. in length and 5 cm. in width to 4·5 cm. in length and 2 cm. in width, the ratio of length to breadth varying from 5 to 1·5. *Flowers* with short pedicels. *Bracts* usually not exceeding the calyx in length, often much smaller. *Caylx* two-thirds the length of the corolla or more, enlarging in the fruiting stage ; sepals linear, densely covered with long, upwardly directed, silky hairs. *Corolla* with a narrow cylindrical basal portion widening gradually in the upper part, regular, with rather small lobes, usually rather more than 1 cm. in length, glabrous or with scattered hairs on the outer surface ; white, faintly scented. *Stamens* more or less equal, much exserted, arising half-way or higher in the tube of the corolla, adnate almost as far as the corolla-lobes, usually with long hairs on the adnate portions of the filaments, these hairs extending for a short distance up the free part of the filament and on to the corolla below. *Style* with stiff hairs in the middle region, sometimes almost

glabrous. Each *nutlet* with a median ridge, slightly tuberculate, with minute glassy hairs on the summits of the tubercles.

Habitat. Sandy places at low elevations.

Flowering season. September to October.

MALMESBURY : Saldanha Bay, *Ecklon and Zeyher* ! *Levyns* 3213 ! St. Helena Bay, *Marloth* 8008 ! Mouth of the Berg River, *Bolus* 6300 ! Theefontein, *Bachmann* 2134 ! Koperfontein *Levyns* 3239 ! Hopefield, *Schlechter* 5303 ! *Bolus* 12774 ! *Bachmann* 1241 ! between Hazenkraal and Matjesfontein, *Bachmann* 1242 ! Grootrivier, *Penther* 1818 ! between Groenkloof and Saldanha Bay, *Drège* 7854 ! Groenkloof, *Zeyher* 1240 ! CAPE : Tygerberg, *Alexander* ! Doorn Hoogte, *Zeyher* ! PAARL : Klapmuts, *Ecklon and Zeyher* ! WITHOUT LOCALITY : *Thunberg* ! *Burmann* !

3. ECHIOSTACHYS ECKLONIANUS Levyns, comb. nov. *Lobostemon Ecklonianus* Buek in Linnaea, xi, p. 144 ; C. H. Wright in Fl. Cap. iv, 2, p. 40. *L. Galpinii* C. H. Wright in Fl. Cap. iv, 2, p. 41. *Echium Ecklonianum* DC. Prod. x, p. 14. *E. Galpinii* I. M. Johnston in Contrib. Gray Herb. n.s. lxiii, p. 52 (1924).

A perennial herb with a somewhat woody underground stem, which may branch occasionally, giving off tufts of leaves and flowering shoots annually. Occasionally reaching 36 cm. in height, but usually much less ; flowering shoot covered with long, weak, spreading hairs. Basal *leaves* oblanceolate, much attenuated at the lower end, somewhat dilated at the extreme base, acute or obtuse, up to 12 cm. long and 18 mm. broad, usually less, with weak spreading hairs on both surfaces tending to fall off with age. Leaves on the flowering shoot smaller than the basal and becoming oblong near the flower. *Inflorescence* 8 cm. long or less and 4 cm. broad or less ; flowers with short pedicels. *Bracts* linear, with indumentum similar to the leaves, 2 cm. or less at the base of the inflorescence, and diminishing in size towards the apex. *Calyx* about three-quarters the length of the corolla, enlarging in fruit ; sepals linear or somewhat spathulate, covered outside with long, upwardly directed hairs. *Corolla* cylindrical at the base, widening very gradually, regular, with obtuse lobes, usually less than 1 cm. in length, with spreading hairs along the centre vein of each lobe or glabrous, purplish or reddish, strongly scented. *Stamens* more or less equal, much exserted, arising about half-way up the corolla-tube, adnate to the corolla-tube for some distance, with long hairs on the adnate portions of the filaments and similar hairs extending for a short distance up the free parts of the filaments and on to the corolla below. *Style* with spreading hairs on the lower two-thirds. Each *nutlet* with a median ridge, almost smooth.

Habitat. Sandy and gravelly places on lower mountain slopes.

Flowering season. August to December.

STELLENBOSCH : near Somerset West, *Ecklon and Zeyher* ! Sir Lowry's Pass, *Bolus* 5208 ! *Schlechter* 5371 ! *Levyns* 3209 ! CALEDON : Houw Hoek, *Galpin* 4349 ! *Bolus* 9944 ! Elgin, *L. Bolus* 20002 in Herb. Bolus ! Viljoen's Pass, *Rogers* 28934 ! Hermanus, *Levyns* 3014 ! *Bolus* 9684 ! *Bolus* 20037 in Herb. Bolus ! BREDASDORP : near Elim, *Bolus* 9999 !

Table I.—*Mutations in* Lobostemon *and* Echiostachys.

	Vegetative Changes.						Floral Changes.					
	Increase in size of plant.	Decrease in size of plant.	Change in type of branching.	Reduction in leaf surface and crowding.	Increase in density of hairs.	Change in type of hairiness.	Reduction in size of flower.	Change in external surface of corolla.	Colour-change in corolla.	Absence of staminal scales.	Change in shape of anther.	Increase in length of stamens.
L. echioides	×	×	×	×	×	×						
L. paniculatus	:	×	:	×	×							
L. horridus	:	×	×	×	×							
L. gracilis	×	×	×	×	×							
L. capitatus	×	×	×	×	:	:						
L. Bolusii	×	:		×	:							
L. trichotomus	×	:	:	×	:	×	×	×	×			
L. hispidus	:	:	×			:	:	:	×			
L. paniculaeformis	:	:	×				×	:	×			
L. Pearsonii												
L. laevigatus							:	:	:	×		
L. glaucophyllus	:									:	:	×
L. hottentoticus					:		×	:	×			
L. argenteus	:	:	×	×	:	:						
L. stachydeus	:	×	:	×	×	×						
L. fruticosus	:	×		×	:	×						
L. curvifolius	×	×	×	×	×	×						
L. lucidus	×	×	×	×	:	×						
L. trigonus	:	:	:	:	:							
L. strigosus												
L. collinus												
L. decorus												
L. Muirii												
L. oederiaefolius												
L. Marlothii												
L. montanus	:	:	:	:	:	:	:	:	:	:	:	×
L. sanguineus												
L. grandiflorus							:					
E. incanus												
E. Ecklonianus	:	:	:	:	:	×						
E. spicatus	:	:	:	:	:	×	:	×		:	×	

TABLE II.

	Section I.	Section II.	Section IV.	Section V.
Primitive, hairy type of plant.	*L. echioides.* ↓	*L. trichotomus.* ↓	*L. fruticosus.* ↓	*L. montanus.* ↓
Plants with almost glabrous leaves : not particularly bristly. ↑ ↓	*L. paniculatus.* ↓	{ *L. glaucophyllus.* *L. Pearsonii.* *L. hottentoticus.* ↓	{ *L. decorus.* *L. Muirii.*	{ *L. sanguineus.* *L. grandiflorus.*
Plants with almost glabrous leaves : wider than in the preceding group with spino-ciliate margins. Habit erect, with scanty branching.	*L. horridus.*	*L. laevigatus.*		

SUMMARY

1. The previous accounts of the genus *Lobostemon* are shown to be inadequate, and a complete revision has been made.

2. A small genus *Echiostachys* is separated from *Lobostemon* on floral and vegetative features.

3. A more precise definition of *Lobostemon* is given, and it is shown that the so-called Lobostemons of Tropical Africa have no claim to inclusion in the genus, which is purely South African.

4. *Lobostemon* is subdivided into five well-marked sections, the characters of which are given.

5. While the sections may be easily recognised, many of the species show ill-defined boundaries.

6. A cytological investigation of half the species of *Lobostemon* and all the species of *Echiostachys* has been made. The basic number of chromosomes is seven in both genera.

A

B

LOBOSTEMON PANICULATUS

C.

D.
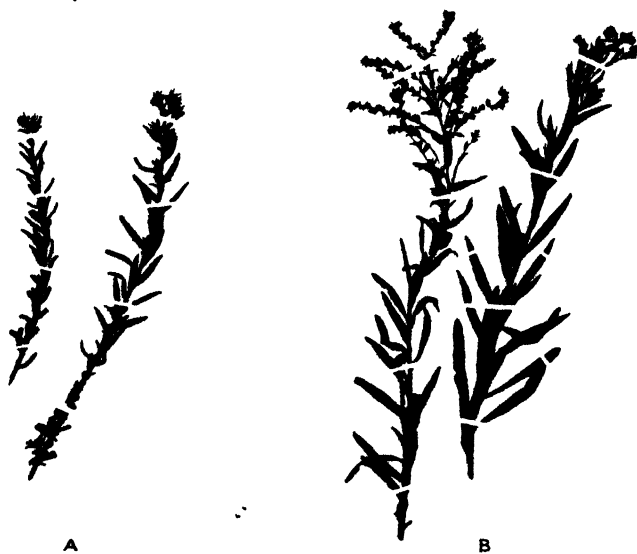
LOBOSTEMON ECHIOIDES

7. The species problem is discussed, and it is shown that Vavilov's Law of Homologous Series in Variation is applicable here.

8. Detailed descriptions of the two genera and the species are given, together with their synonymy.   Herbarium specimens are cited under each species.

9. Keys to the species are given.

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EXPLANATION OF PLATE 29.

Lobostemon paniculatus.—Specimens collected from the same plant : A in July and B in October.

Lobostemon echioides.—C, small-leafed plant ; D, normal plant.

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A study of *Veronica* from the viewpoint of certain floral characters. By
   EDITH R. SAUNDERS, F.L.S., sometime Fellow of Newnham College,
   Cambridge.

(With 67 Text-figures)

[Read 11 May 1933]

In a recent account of a genetical investigation carried out on *Lobelia Erinus* L.
(13) I compared the interrelations of certain petal characters in this genus with
those observed by W. and A. Bateson (1) to exist between the ground-colour
pattern and segmentation in the corolla of *Veronica*. It was owing to the
renewed consideration thus entailed of these authors' observations on the
occurrence of meristic variations in *Veronica* flowers, that the idea took shape
that with our greater knowledge today of floral anatomy it should be possible
to arrive at a fuller understanding of such variations through a study of the
variations in vascular anatomy, which must necessarily accompany gross
aberrations of this order. From this aspect *Veronica** appeared to offer
particularly favourable material for investigation. Moreover, such a study
might well throw further light on the phylogenetic relations of this whole
group of forms.

As is well known, the typical *Veronica* flower is tetramerous, both in calyx
and corolla. The grounds upon which it is now fully accepted, that this
tetramerous condition is not primitive, but has been derived from an original
pentamerous ground-plan through the two processes of suppression of the
posterior sepal and the complete fusion of the two postero-lateral petals, are
too familiar to require detailed re-statement here. But it may be well to focus
attention on two points. Firstly, as regards the calyx, there is the fact that
five sepals are normally present in some forms, viz. the few species constituting
the European-Asiatic section *Paederota* and the small New Zealand section
Pygmaea; individual species in other sections, e.g. *V. satureioides* Vis.
(*Veronicastrum-Fruticulosae*), *V. Teucrium* L., *V. austriaca* L., *V. multifida* Jacq.,
V. prostrata L., *V. nivea* Lindl. (*Chamaedrys-Pentasepalae*) †, *V. Derwentia* Andr.,
V. densifolia F. Muell., *V. formosa* R. Br. (*Labiatoides*) ‡. To this list can now

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* Here used in its widest sense to include *Paederota, Leptandra. Hebe,* and *Pygmaea.*

† *V. orientalis* Ait. is also included by some authors in the pentasepalous division of the
section *Chamaedrys*. I have not been able to obtain material in quantity of the type form,
but in two varieties (*tenuifolia* and *Whittalii*) K 5, though not uncommon, was not a con-
stant character. In the scheme of classification recently proposed by Römpp (12) *orientalis*
is excluded from the pentasepalous subsection (see the following footnote).

‡ The classification here cited, apart from the sections *Paederota, Leptandra, Hebe,* and
Pygmaea, is that proposed by H. Römpp (12) except in the one respect that *multifida* has been
retained in the pentasepalous division of *Chamaedrys*.
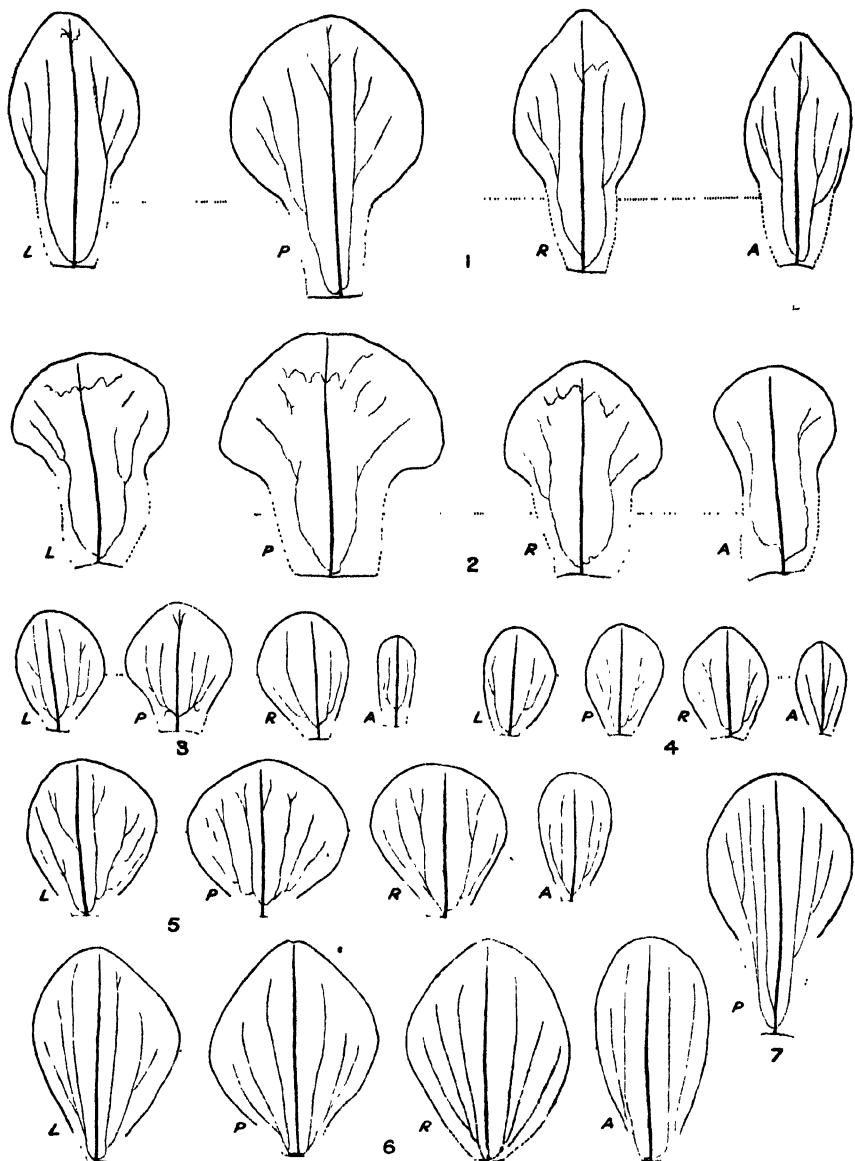
Figs. 1–6.—The four petals from individual flowers of species of *Veronica* characterized by a single midrib in the posterior segment. 1, *V. longifolia* L. 2, *V. hybrida* L. 3, *V. serpyllifolia* L. 4, *V. hederifolia* L. 5, *V. repens* Clar. 6, *V. glauca* Sibth. & Sm. Fig. 7, Posterior corolla segment with a single midrib bundle from a flower of *V. decumbens* Armstr.; a species producing some flowers with a 1-midribbed and others with a 2-midribbed posterior segment, the former being less numerous than the latter. (Compare text-figs. 21 *a–d*.) In several instances some of the smaller veins have become detached through disappearance of the connecting link with the main system. (See text-figs. 2 L, 2 P, 2 R, 4 R, 5 P.)

In the above and all succeeding figures in the present account the letters L, P, R, and A indicate the left lateral petal, the posterior corolla segment, the right lateral, and the anterior petal respectively.

All figures of corollas and of individual petals have been drawn throughout to the same scale of magnification, except text-figs. 14 *a*, *b*, which are rather more highly magnified.

be added two East African species recently described by R. E. Fries, viz. *V. keniensis* and *V. aberdarica* (*Veronicastrum-Glandulosae*). It is to be noted, however, that some tetrasepalous flowers have been observed in several, and very probably occur occasionally in all the above-named species. Besides those species in which K 5 is typical, many normally tetrasepalous species occasionally produce flowers with a five-membered calyx *. This was observed in *V. alpina* L. (*Veronicastrum-Alpinae*), *V. fruticans* Jacq. (*Veronicastrum-Fruticulosae*), *V. longifolia* L. and var. *rosea* (*Pseudolysimachia*), *V. Buxbaumii* Ten.† (*Alsinebe-Agrestes*), *V. pectinata* L. (*Chamaedrys-Strictiflorae*), *V. Beccabunga* L. (*Beccabunga*), *V. Darwiniana* Colenso, *V. Hulkeana* F. Muell., *V. loganioides* Armstr. (*Hebe*), and has been recorded by other writers in *V. latifolia* L. (*Chamaedrys-Multiflorae*), and other species‡. Secondly, the position as regards the corolla is precisely similar. Five petals are characteristic in *Pygmaea* ; the same number has been found by R. E. Fries to be typical in four East African species, viz. the two pentasepalous species *keniensis* and *aberdarica* cited above and the two tetrasepalous species *V. linnaeoides* R. E. Fries and *V. Battiscombei* R. E. Fries. Lack of conformity between sepal and petal numbers is not confined to the two last-named species. The converse combination K 5 C 4 is characteristic of the whole pentasepalous division of *Chamaedrys*, of the bulk of the flowers in *V.* (*Paederota*) *Bonarota* L., and of occasional flowers in a number of other species.

The observations of W. and A. Bateson referred to above, which were later carried further by W. Bateson and D. F. M. Pertz (2), were directed to ascertaining the extent, frequency, and heritability of meristic variations occurring chiefly in the corolla, *V. Buxbaumii* being the species most extensively studied §. These observers found that in a small. percentage of flowers in this species the corolla was segmented into more than the normal number of lobes (five or even more) or into fewer (three or even two). When the petal lobes were reduced to two, one was posterior and one anterior. Three-petalled corollas had almost invariably an unpaired posterior lobe ‖. The pentamerous condition was produced by duplication of one of the four ordinary segments.

* Often to be found among the earliest flowers of the season.

† See footnote §, below.

‡ Literature relating to *Veronica* having been cited in recent accounts by Römpp (12), Zamelis and Melderis (14), and Graze (9), the reader is referred to these authors for other references than those given here.

§ At the time of these observations the specific name *Buxbaumii* had not been superseded. In order to avoid the confusion which might possibly arise if this name were retained in the present account when referring to these experiments, and was replaced elsewhere by *persica*, the synonym now in use, the name *Buxbaumii* has been employed throughout.

‖ Bateson and Pertz observed a case of the rare condition in which the unpaired member was anterior (2, fig. 6). Similarly, among the many three-petalled flowers which I have examined, I have only once found an instance of this arrangement, which occurred in *Cymbalaria*. It may be added that C 3 may arise, though also rarely, from a different cause, viz. fusion instead of suppression. A corolla so produced differs from those arising from the latter cause in having no plane of symmetry.

In view of the accepted origin of the posterior segment in the normal flower, it might have been anticipated that this member would invariably be the one to be duplicated. It was found, however, that duplication of both anterior and lateral petals was also frequent. Though it is to anticipate, it may be
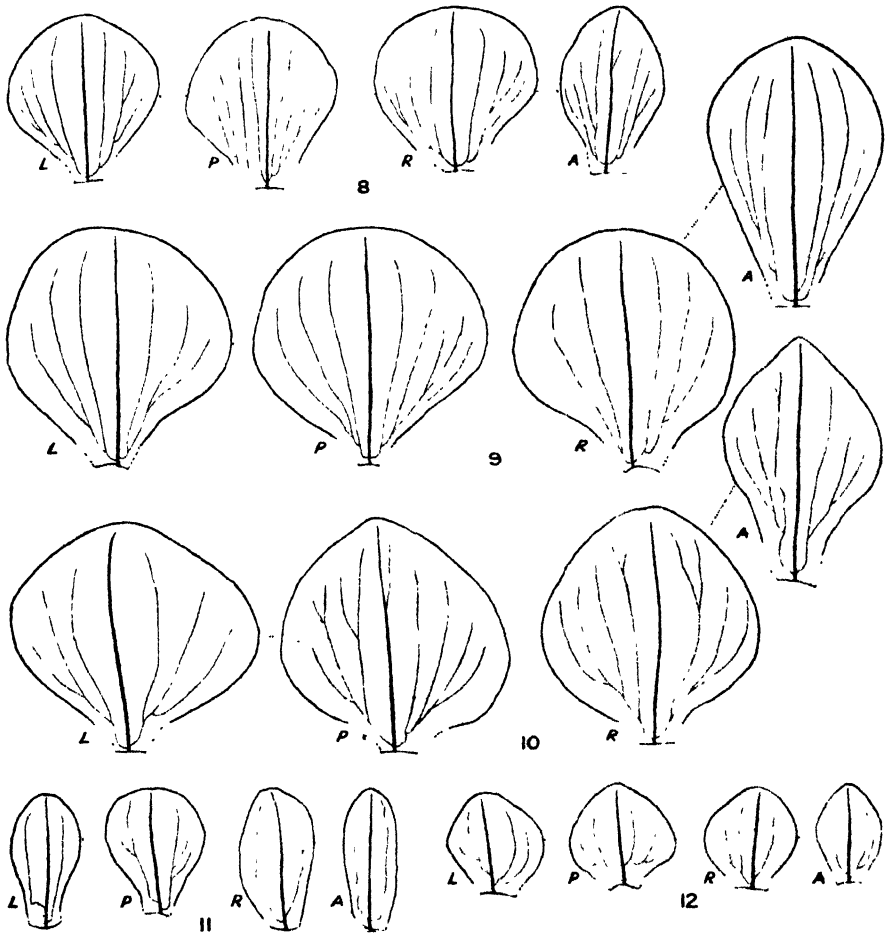
Figs. 8-12.—The four petals from individual *Veronica* flowers, with a 1-midribbed posterior segment. 8-11, from species producing some flowers with a 1-midribbed and others with a 2-midribbed posterior segment. 8, *V. Buxbaumii* Ten. 9, *V. filiformis* Sm. 10, *V. filifolia* Lipsky. 11, *V. Beccabunga* L. 12, *V. Anagallis* L., a species characterized, like those shown in text-figs. 1-6, by flowers with a 1-midribbed posterior corolla segment. Detached vascular strands are to be seen in text-figs. 9 P & 11 R.

stated here that the relative frequency of occurrence of duplication, in any particular species, of the anterior or of a lateral member as compared with that of the posterior segment (=reversion) is determined, at least in part, by the

particular form of vascular scheme typical of the posterior segment in the normal flowers of that species ; consequently reversionary duplication is found more frequently in some species, non-reversionary in others (see later, p. 490). The six-petalled flower is produced by the simultaneous duplication of two of the ordinary members of the corolla. The above relations in regard to petal number and disposition are readily ascertainable by mere inspection, but if any advance was to be made beyond the point to which this method of investigation brings us, it was clearly desirable to discover what variations in the vascular scheme underlie these departures from type. The results of investigations undertaken with this object in view form the subject-matter of the present account.

A series of sections taken through normal *Veronica* flowers show those relations with which we are now familiar in many other genera. Sepal midrib bundles issue from the central cylinder on equidistant radii. In many species they remain unbranched for a considerable distance, only giving rise in the distal region, if at all, to a net-work of veins (for occasional exceptions to this behaviour, see below). The arrangement of the sepals in regard to one another in the tetrasepalous flower is as follows. One of the antero-lateral pair, the right in some flowers, the left in others, overlaps both its neighbours. The diagonally opposite postero-lateral member is overlapped by its two neighbours. Each of the other two sepals overlaps its neighbour on the one side, and is overlapped by its other neighbour on the other edge (text-fig 48 *a*). The midrib bundle of the wholly outer sepal issues from the central cylinder slightly in advance of the others ; that for the fifth (posterior) sepal (if present) somewhat after the other four. In the most fully developed tetrasepalous types all four sepals are furnished with marginal veins, but in individual cases (? species) one or both of the postero-lateral members may lack the marginal on the side towards the median plane. When a fifth sepal is developed, it, like the others, may possess two marginal veins, or it may lack one or both (text-fig. 43). These variations are possibly governed by the special exigencies of space or/and time particular to each individual (or species). *In all the species examined these marginals are typically commissural in origin.* The adjacent marginals of two neighbouring sepals arise conjoined with each other as components of a trunk cord composed of them and of a petal midrib bundle, these trunk cords alternating with the sepal midribs (text-figs. 44 *a–c*, 45 *a*, *b*, 63 *a*, *b*). This relation was observed by Juel (10), who describes the petal veins as originating at the point of bifurcation of bundles, which in this way provide the marginal veins of the sepals.

In the exceptional case in which a sepal does not receive one or other commissural marginal, this lack may be made good by true lateral branching of the midrib (text-figs. 42, 57). Thus it sometimes happens that, although all the sepals of a flower are alike in that each shows the usual pair of marginal veins, these veins may not all have had the same origin. In other words, a similar final appearance may be brought about by means of a quite different cell lineage. One sees here but one more illustration of the fact that when the
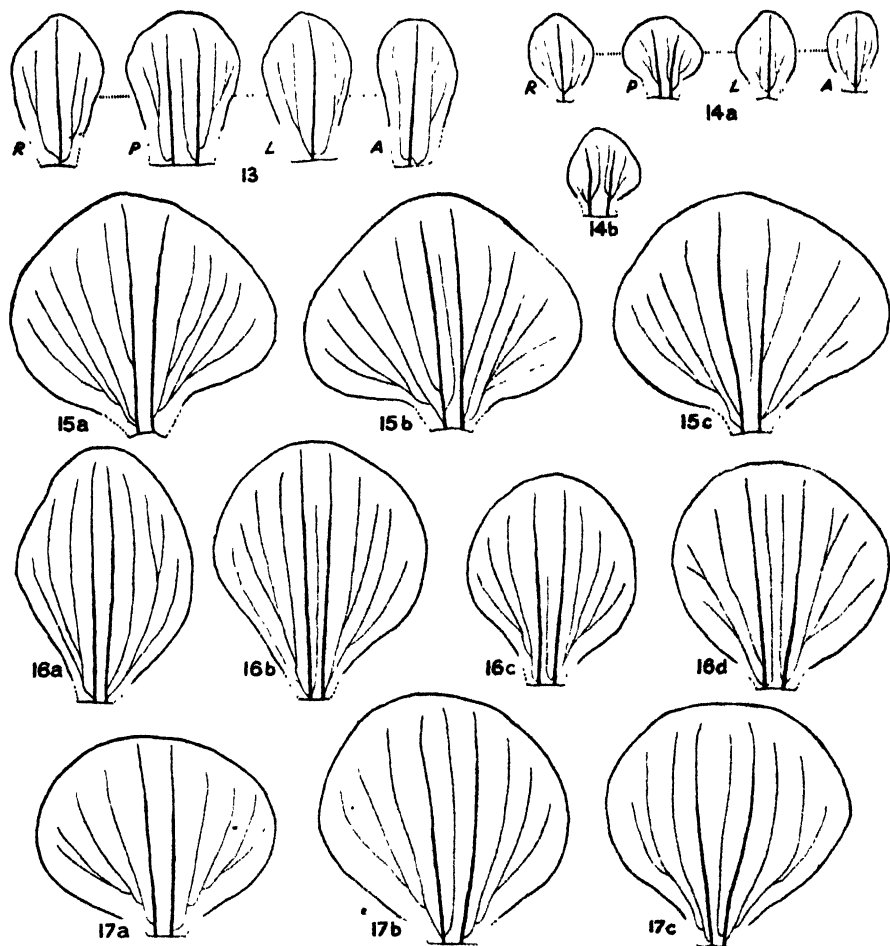
Figs. 13–17.—Petals from species of *Veronica* which commonly produce some flowers with a 1-midribbed and some with a 2-midribbed posterior corolla segment or from species which produce almost exclusively flowers with two midrib bundles in this segment. 13, *V. alpina* L. The four petals from a flower with two midrib bundles in the posterior segment, the left bundle branching unilaterally, the right, bilaterally. 14 *a*, *b*, *V. arvensis* L. ; *a*, the four petals from a flower with two midrib bundles in the posterior segment branching as in 13 ; *b*, posterior segment with two midrib bundles from another flower. Both bundles bilaterally branched. 15 *a–c*, *V. filifolia* Lipsky. Three posterior segments each with two midrib bundles. *a*, both midrib bundles branched unilaterally ; *b*, left midrib bundle branched bilaterally, right, unilaterally ; *c*, branching unequal as in *b*, but the central strand having become detached it is uncertain which of the two midribs has branched bilaterally and which unilaterally. 16 *a–d*, *V. cinerea* Boiss. & Bal. Four posterior segments each with two midrib bundles ; *a*, both bundles branched unilaterally ; *b*, left bundle branched bilaterally, right unilaterally ; *c*, right bundle branched bilaterally, left unilaterally ; *d*, both bundles branched bilaterally. 17 *a–c*, *V. filiformis* Sm. Three posterior segments. Branching as in 16 *a–c*.

hereditary mechanism controlling development for some reason ' goes wrong ', an attempt to make good the defect by some compensating adjustment leads to the formation of a more or less normal structure.

The vascular system of the corolla calls for little comment so far as the anterior and lateral petals are concerned. Normally, whatever the species, a single strand detached, as stated above, from each trunk cord issuing on the anterior and lateral radii becomes the single midrib bundle of the corresponding petals. This bundle branches more or less equally on either side, giving rise to a single system. In the posterior segment, on the other hand, the vascular scheme shows a variety of patterns. These fall naturally into two classes. In the one class the whole vascular supply constitutes a single, in the other a double, system. These two patterns are conveniently distinguished as simplex and duplex. In the simplex form a single bundle enters the petal segment and branches bilaterally as in the other members of the corolla (text-figs. 1–12). In the duplex two separate bundles, *arising on different radii*, enter the petal segment (text-figs. 13–20 and 21 *b–d*)*. Each of the two bundles gives rise to its own system of lateral veins, the two systems usually remaining distinct throughout. This latter type of venation is characteristic of species normally having five-sepalled flowers, and also of the individual five-sepalled flowers occasionally occurring in species which are typically four-sepalled. Nor is the reason for this regular association far to seek. For in such flowers the midrib bundle for the posterior sepal issues from the central cylinder in the mid-line, hence the vascular elements emerging later for the superposed petal segment must necessarily pass out of the vascular cylinder to right and left of the gap so formed, thus giving rise to duplicate systems. On reference to the Table facing p. 472 it will be seen that the records for seven five-sepalled species (*armena*, *austriaca*, *prostrata*, *Teucrium*, *nivea*, *Derwentia*, *satureioides*), in which a total of more than a thousand normal corollas were examined, show without exception a double vascular system in the posterior petal segment. In one other five-sepalled species (*multifida*) two flowers out of a total of 64 were recorded as having a single system. Unfortunately the sepal number in these two exceptional flowers was not observed, but I more than suspect that they will also have been exceptional in lacking the fifth posterior sepal (see later, p. 481) †, for, as has been stated, it is not uncommon for five-sepalled species to produce an occasional four-sepalled flower. Such flowers were noticed in *austriaca*, *prostrata*, and *nivea*. Where the posterior sepal is lacking the way is opened for the passage outwards of a single median petal bundle. Hence we find that most four-sepalled species bear a proportion of flowers with a 1-midribbed as well as those with a 2-midribbed posterior corolla segment, and that some bear only flowers of the former type.

* In some pentasepalous species the dual origin of the two systems is obscured owing to the fact that the two midribs arise in contact with the posterior sepal midrib, the three bundles at first forming a single thick cord.

† The fact that Römpp (12) definitely excludes *multifida* from the pentasepalous division of *Chamaedrys* gives support to this supposition.
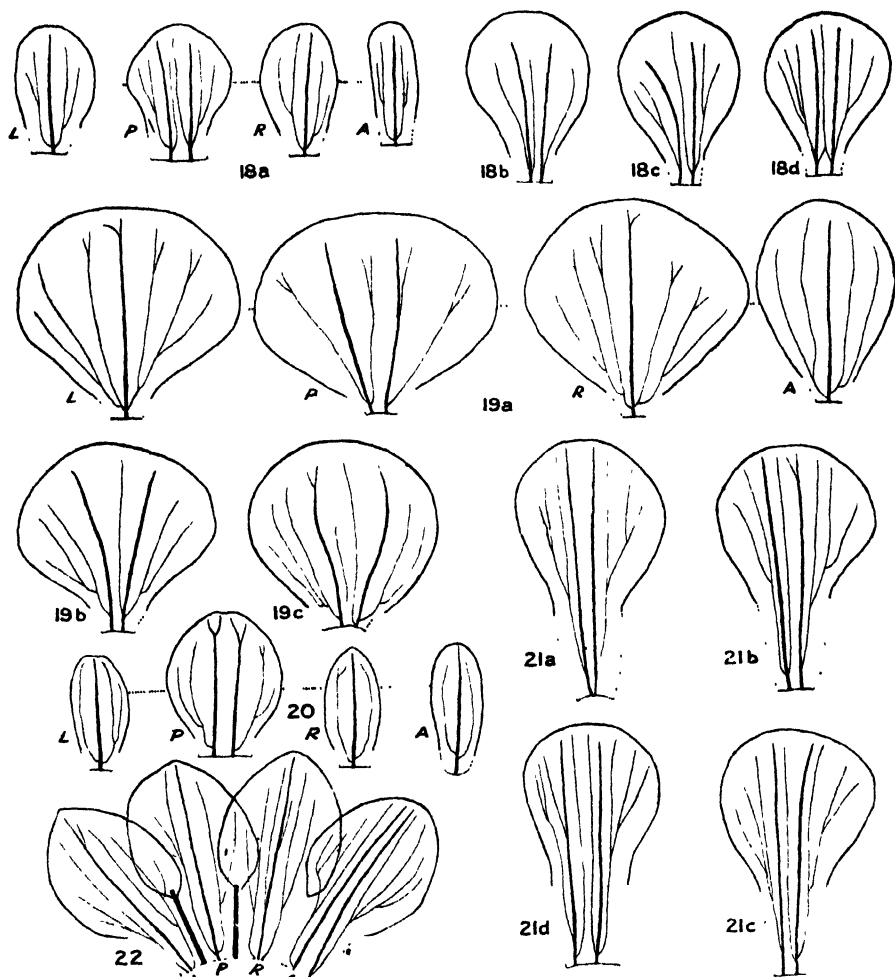
Figs. 18–21.—Petals from species of *Veronica* which commonly produce some flowers with a 1-midribbed and some with a 2-midribbed posterior corolla segment (continued). 18 *a–d*, *V. officinalis* L.; 18 *a*, the four petals from a flower with two midrib bundles in the posterior segment, both bilaterally branched; *b–d*, three posterior segments each with two midrib bundles, in *b* left bundle branched bilaterally, in *c* right bundle branched bilaterally, in *d* a false mid-vein formed by the junction of a branch from each midrib. 19 *a–c*, *V. Chamaedrys* L.; *a*, the four petals from a flower with two midrib bundles in the posterior segment, the left bundle branched bilaterally, the right unilaterally; in *b* the right bundle, in *c* both bundles branched bilaterally, but the inner branch from the left midrib is seen detached, having failed to differentiate in continuity with the midrib. 20, *V. Beccabunga* L. The four petals from a flower with two midrib bundles in the posterior segment, both unilaterally branched. 21 *a–d*, *V. decumbens* Armst. Four posterior segments. In *a* two bundles converging towards the base forming an open V thus **V**, probably derived from the bifurcation of a single bundle. In *b*, *c*, *d* two midrib bundles showing the usual types of branching. Fig. 22, *V. vernicosa* Hook. f. An exceptional corolla showing duplication of the midrib in the anterior segment. (Compare text-figs. 59 *a*, *b*.) Posterior segment with one midrib. [The lower portion of the tube has been cut away, hence the origin of the lateral veins from the midrib in the two lateral petals is not seen.]

The fact that the posterior corolla segment in some species of *Veronica* is furnished with two main veins was first observed by Duvau in 1826. Adhering to the arrangement of Linnaeus in which the species are classified into three groups, (1) with terminal flower spikes, (2) with lateral spikes, (3) with solitary flowers, Duvau concluded, after investigating 81 species, that the single-veined condition of the back petal was characteristic of those included in group 1, and the double-veined of those in group 2, while those in the third and largest group were mixed. He acknowledged, however, that this distinction between groups 1 and 2 was not invariable, for of the 37 species examined belonging to group 1 seven had flowers in which the back petal was double-veined, and of the 34 examined in group 2 three had flowers in which this petal was single-veined. Duvau, further, surprisingly concluded that the presence of two main veins could not be used to support an interpretation of the derivation of the two-veined posterior corolla segment from the suturing of two petals, since such a conception would imply a loss of regularity, by which I take him to mean that it would presuppose a variable corolla ground-plan in the genus. Duvau's original observation was later confirmed by Moquin-Tandon (1856), who took a contrary view, holding that the presence of the two bundles indicated an origin from two petals united in one. This interpretation was disputed at the time by Duchartre, while Chatin, though believing that the presence of five veins in the 4-lobed corolla indicated an origin from five petals, took the curious standpoint that the difficulty lay in determining which structure had arisen from the union of two*. No further reference to an interpretation of the *Veronica* corolla based on the vascular system appears to have been made until 1887, when Camus again drew attention to the presence of two veins in the posterior petal segment, adding the comment that it was a characteristic which did not appear to have been sufficiently taken into account. He asks the question—Does the occurrence of these two veins result from fusion or deduplication? But goes no further in reply than to observe that it is difficult to say. In 1891 Juel, as the result of a fresh examination of the venation system of the corolla, came to the conclusion that the number of veins in the back petal is a character of systematic importance, for, he states, a classification in accordance with this character proves to be consistent with the natural grouping of the species. Adopting the scheme of classification in which all species are grouped into the following seven sections—*Hebe* Juss., *Leptandra* Nutt., *Pseudolysimachia* Koch, *Beccabunga* Griseb., *Chamaedrys* Griseb., *Veronicastrum* Benth., *Omphalospora* Bess.—and sorting the species examined in each section into two categories according as the corolla was 4-veined or 5-veined, i.e. according as the back petal was furnished with one or two main veins, Juel noticed that the species belonging to the section *Hebe*

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* The opinions here cited of Moquin-Tandon, Chatin, and Duchartre were expressed in the course of a discussion upon some monstrous flowers of *Veronica Teucrium* described by the last-named observer (see 4).
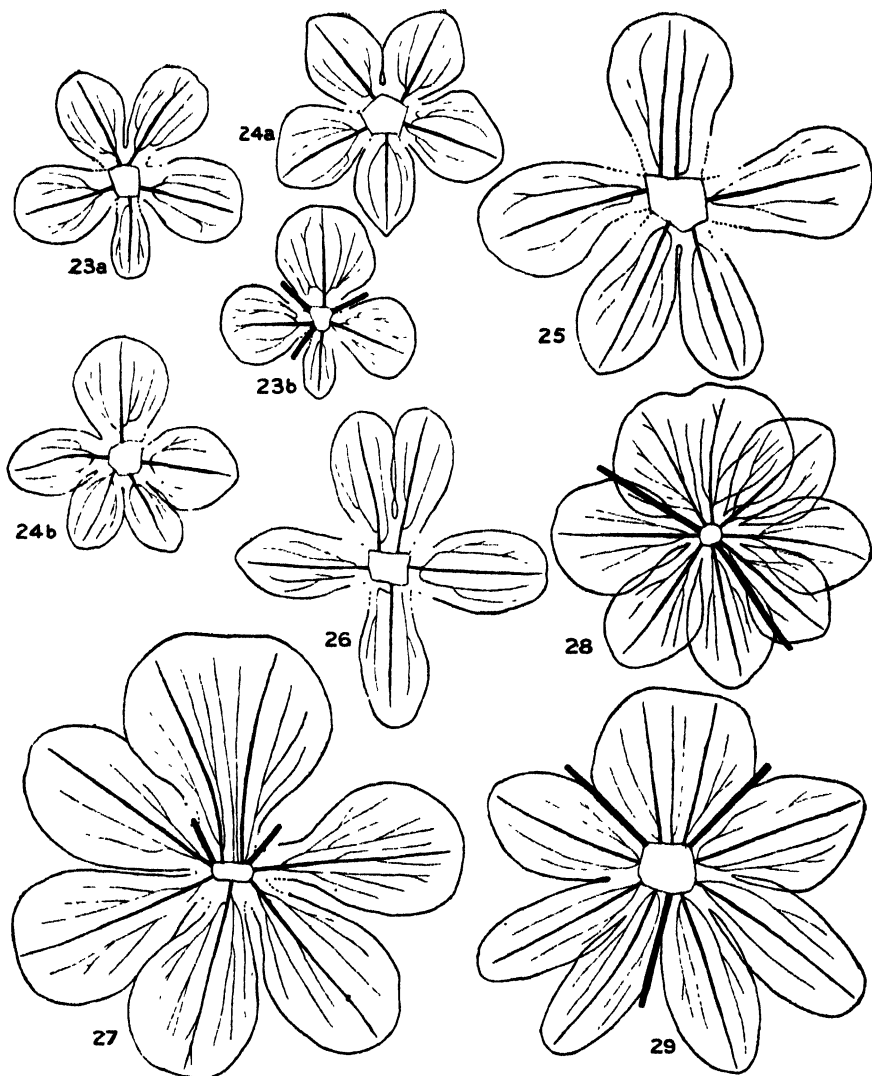
Figs. 23–29.—From exceptional *Veronica* flowers showing reversion in regard to petals or
stamens or both, or unconformable pleiomery of various kinds in the corolla.
23 *a*, *b*, *V. serpyllifolia* L.; *a*, C 5 corolla with two postero-lateral petals; *b*, normal
corolla with an extra stamen; posterior segment with one midrib bundle. 24 *a*, *b*,
V. Anagallis L.; *a*, C 5 corolla with two postero-lateral petals; *b*, C 5 corolla
due to duplication of the anterior petal; posterior segment with one midrib
bundle. [In these and similar species reversion in the corolla (*a*) is far less fre-
quent than unconformable types of pleiomery (*b*).] 25, *V. alpina* L. C 5 corolla
due to duplication of the anterior petal. Posterior segment with two midrib
bundles. 26, *V. Beccabunga* L. C 5 corolla with two postero-lateral petals.
27, *V. fruticans* Jacq. A C 6 m 7 corolla. 28, *V. cinerea* Boiss. & Bal. A C 7 m 8
corolla with one front and one back stamen. 29, *V. loganioides* Armstr. A C 7
corolla with unusual veining in the posterior segment from a flower with one
front and two back stamens. Here and in all later figures m = midrib. For use
of the term ' unconformable ', see p. 477.

with the exception of *elliptica*, to *Leptandra* and to *Chamaedrys*, with the exception of *Aucheri*, had a 5-veined corolla, those belonging to *Pseudolysimachia* and *Beccabunga* a 4-veined corolla. The sections *Veronicastrum* and *Omphalospora*, on the other hand, included both 4-veined and 5-veined species, the two forms being listed in each subsection in *Veronicastrum*, in different subsections in *Omphalospora*. Although Juel examined a considerable number of species, the number of flowers recorded was sometimes quite small. From the fuller data given in the present account it will be apparent that the degree of accord between the type of venation of the posterior corolla segment and systematic relationship is by no means so close as Juel's presentation of the position would suggest.

Leaving further consideration of the perianth for the moment, however, we may briefly consider the staminal and carpellary whorls. The bundles for the two stamens leave the central cylinder separately and independently in line with the two postero-lateral sepals (text-figs. 45 *a*, 49 *b*, 53 *c*, and others). When, as occasionally happens, one of the two missing front stamens is developed the corresponding bundle similarly arises separately and independently, in line with an antero-lateral sepal (text-figs 23 *b* & 30) *. The residual vascular tissue serves the gynoecium. Two bundles which turn outwards in the median plane, and usually give off a pair of lateral veins below the loculi, become the midribs of two sterile valve carpels. The remaining vascular elements left behind in the centre differentiate into the bundles of two lateral fertile carpels (text-figs. 44 *b*, *c*, 45 *a*, *b*, 47, and others). The typical gynoecium will therefore be represented by G 2+2. In certain species an appreciable interval occurs between the out-turning and branching of the two median sterile carpel midribs and the differentiation of the two lateral fertile bundles, so that a short but definite internode is recognisable in which the residual vascular tissue consists of a central stele composed of a core of xylem surrounded by phloem (text-fig. 59 *c*). This is wholly irreconcilable with the view that the gynoecium is constructed of only two carpels. On the view that it is composed of two pairs of carpels this difference in time of development is quite natural. Exceptionally, both carpel whorls may be trimerous, a reversionary condition, we may suppose, comparable with that now and again occurring in the androecium. Another exceptional condition observed in only two flowers out of the whole number examined † is that in which the styles of a normal ovary were not connate, but, although fully and equally developed, were separate throughout their length.

We are now in a position to consider further the variations in the vascular scheme of the posterior corolla segment and those variations in segmentation which result in pleiomerous and oligomerous corollas. An examination of corollas with a 2-veined posterior segment soon reveals that the double venation

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* The development of *both* front stamens in an otherwise normal flower was observed only once and occurred in *cataractae*.

† One in *Buxbaumii* and the other in *Teucrium* var. *thracica*.
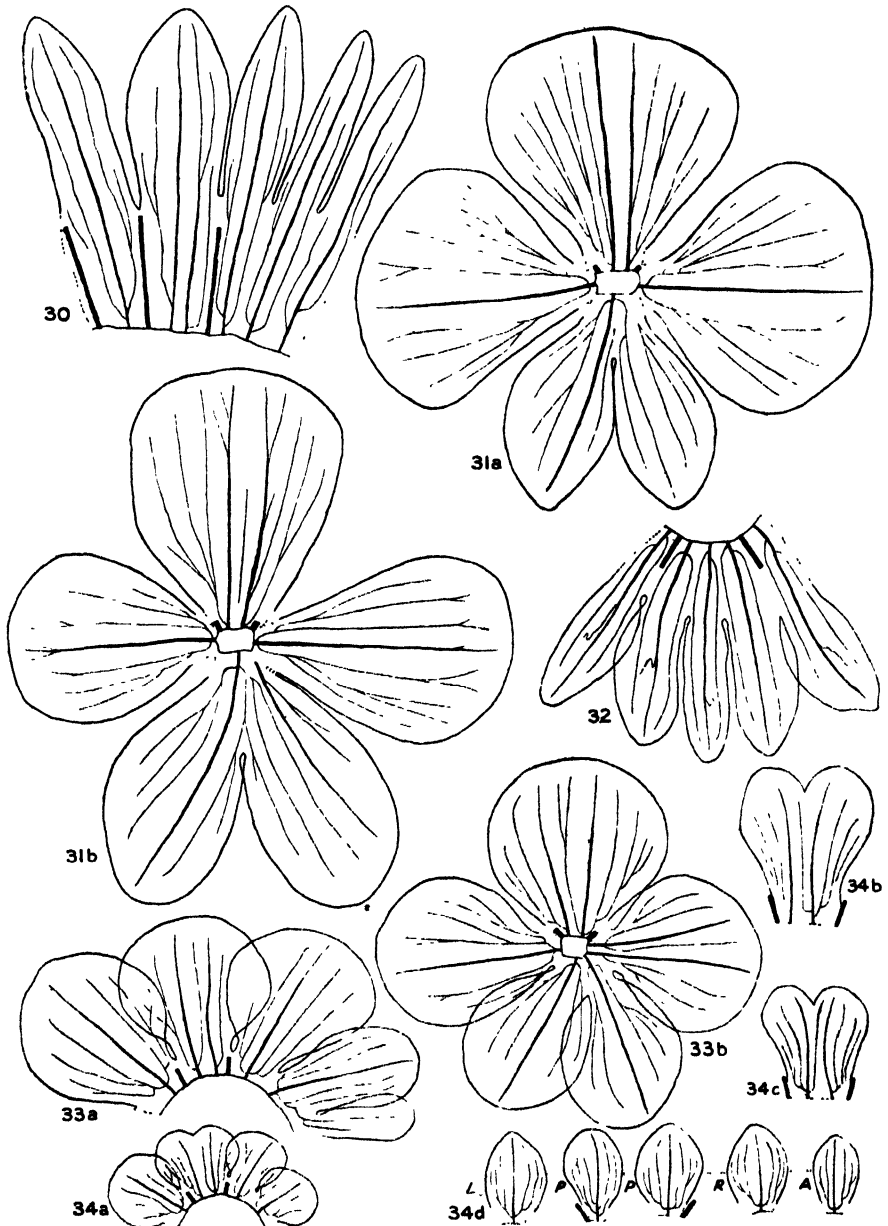
Figs. 30–34.—Exceptional *Veronica* corollas due to unconformable pleiomery of various
kinds or to reversion. 30, a derivative of *V. spicata*. The corolla split down one
side. The posterior segment with two midrib bundles, the anterior petal dupli-
cated. An antero-lateral stamen is present in addition to the usual two postero-
lateral members of the androecium. 31 *a, b, V. peduncularis* M. Bieb. *a,* corolla of
five lobes owing to duplication of the anterior petal. Segmentation and vascular
development imperfectly adjusted, the two similar anterior lobes being supplied

by a common vascular system. One strand of this sytem is seen disconnected from the rest. Posterior segment with two midrib bundles. *b*, corolla as in *a*, but the two anterior petals are supplied with separate vascular systems, nevertheless the adjustment between segmentation and vascular development is not quite perfect, a strand originating from the system in the left anterior member extending into the right anterior member. 32, *V. spicata* L. The corolla, which has been split down the back, showing complete reversion. 33 *a*, *b*, *V. Buxbaumii* Ten. *a*, corolla of five lobes owing to duplication of the anterior petal, the two unequal lobes supplied by a common vascular system. (Compare text-fig. 31 *a*.) Posterior segment with two midrib bundles. *b*, corolla of five lobes owing to duplication either of the anterior or of the left lateral petal. Segmentation and vascular development show complete accord. 34 *a–d*, *V. polita* Fries. *a*, a corolla showing a first step towards reversion in the slight bilobing of the posterior segment. *b*, *c*, posterior segments from two corollas rather more deeply bilobed. Segmentation and vascular development in both cases show imperfect adjustment. *d*, the five petals of a flower showing complete reversion and adjustment of segmentation and vascular development.

system reaches very different degrees of development, not only between one species and another, but between one flower and another on the same individual. In the simplest case the two midrib bundles, as they pursue a nearly parallel upward course, give off lateral branches to one side only, the side toward the petal margin, the two systems being about equally developed and more or less the counterpart of one another (text-figs. 15 *a*, 16 *a*, 17 *a*, 20). If development is somewhat more vigorous, one midrib, as in the preceding case, branches only on the outer side, but the other branches on both sides. Examples coming under this head can be classified as ' rights ' and ' lefts ', respectively (text-figs. 13, 14 *a*, 15 *b*, 16 *b*, *c*, 18 *b*, *c*, 19 *a*, *b*, 21 *b*, *c*), the two patterns occurring on the average with about equal frequency. In still more highly developed forms both midribs branch bilaterally. In the great majority of this class the two systems, as in the two preceding cases, remain distinct throughout (text-figs. 14 *b*, 16 *d*, 18 *a*, 21 *d*). In a minority of flowers, however, one meets with posterior petal segments in which two lateral veins, the lowest formed by each of the two midribs on the side towards the median plane, meet and thenceforward continue upward as a single strand, thus giving rise to a false mid-vein (text-fig. 18 *d*). In many species in which this latter condition was observed, as well as in several in which only one of the two midribs, as a rule, is bilaterally branched, it is not unusual to find some corollas with a single weak vein between the two midribs showing no connection with either. In this unexpected appearance we have an important clue to the way in which the successive stages in reduction of the vascular system in the posterior petal segment have come about, a point to which I shall return shortly.

Besides the above well-marked patterns, which are widely distributed, another, which bridges the gap between the typical single system and the lowest grade of the double system, is met with in some species in the section
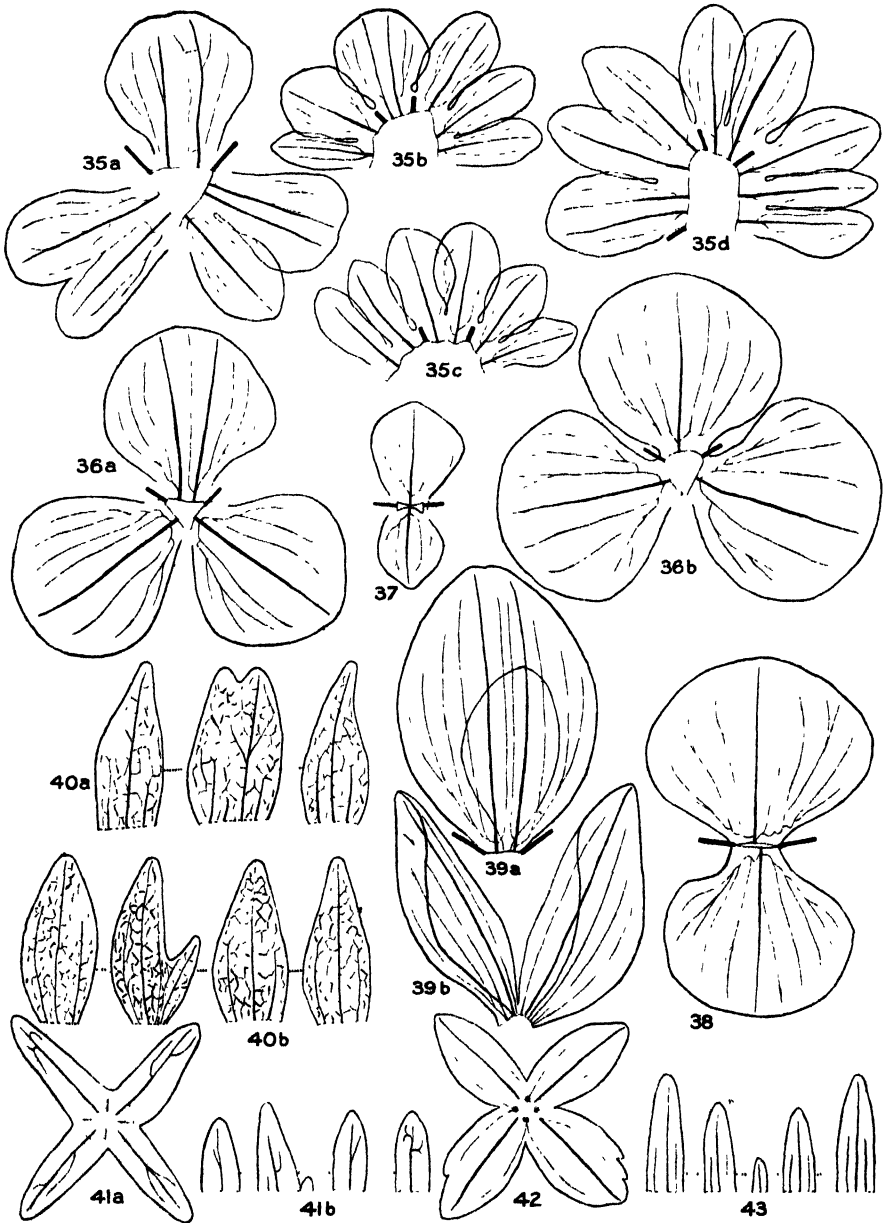
Figs. 35–39.—Exceptional *Veronica* corollas due to unconformable pleiomery of various kinds or to oligomery. 35 *a–d, V. Beccabunga* L. *a*, a C 5 m 7 corolla. Posterior and right lateral segments each with two midrib bundles. Left lateral segment bilobed, showing imperfect adjustment of segmentation and vascular development. *b*, a C 6 m 7 corolla showing simultaneous duplication of two petals. Posterior segment with two midrib bundles. *c*, a C 6 m 6 corolla showing both reversion and duplication of a lateral petal. *d*, a C 8 m 9 corolla with three stamens due

possibly to a combination of partial ' twinning ' and reversion. 36 *a, b, V. Bux-baumii* Ten. Trimerous corollas owing to suppression of the anterior petal. *a,* posterior segment with two midrib bundles (usual form). *b,* posterior segment with one midrib bundle (rare form). 37, 38, dimerous corollas owing to suppression of both lateral petals. 37, *V. serpyllifolia* L. 38, *V. Buxbaumii* Ten. 39 *a, b, V. Teucrium* var. *thracica* Velenovsky. The posterior segments of two corollas showing ingrowth of the meeting edges of the two component petals. *a,* the ingrown edges completely conjoined forming a superposed flap. *b,* the ingrown edges free and turned over so that the two petals come to stand back to back (see also text-figs. 55 *a, b*). Figs. 40–42, exceptional forms of the calyx from various species of *Veronica.* 40 *a, b, V. Buxbaumii* Ten. *a,* calyx of three segments owing to the almost complete fusion of two of the normal four sepals as shown by the scheme of venation and the slight bilobing (compare text-fig. 58). *b,* calyx of four segments, showing partial reversion to K 5 with imperfect adjustment of segmentation and vascular development (compare text-fig. 57). [Only the free portions of the sepals are represented.] 41 *a, b, V. gillesiana* T. Kirk. *a,* axis with calyx viewed from above. Sepals without marginal veins. In the centre the disc (indicated by dotted circle) and the four bundles for the petals. *b,* the free portions of the sepals from another flower showing a small fifth member without vascular system. 42, *V. polita* Fries. Axis with calyx viewed from above. Sepals with marginal veins arising sometimes commissurally, sometimes by true lateral branching of the midrib. The two front sepals with one margin toothed. Fig. 43, *V. orientalis* var. *tenuifolia* Boiss. The free portions of the sepals of a 5-membered calyx. The small fifth sepal with midrib, but without marginal veins.

Hebe. In this intermediate grade only one bundle leaves the central cylinder for the posterior segment, but at some point at, below, or above the exsertion level of the segment this strand forks. When the fork occurs below the exsertion level it is usually possible, nevertheless, to refer the detached corolla to its proper grade. For when the vascular supply of the posterior segment is *genuinely* double the two midribs follow a parallel upward course, whereas when a single strand forks before it enters the segment the course of the two resulting bundles is divergent, hence in the detached corolla they appear as an open V thus \/ (text-fig. 21 *a*). Where this appearance gives rise to doubt, a cross-section taken through the axis just below the exsertion level at once decides the point. In practice, however, the number of cases in which the appearance in the detached corolla leads to uncertainty are so few that the inspection method of recording rarely needs checking in this way. Intermediate conditions between the other venation patterns described above also occur now and again : as, for example, when the double system in a segment differs from the typical grade in which the two midribs branch only on the outer side in that one midrib gives rise, in addition, to a single very short branch to the inside, quite near the apex : or, again, when one of the two midribs present branches normally on the outer side and has one short stump of a branch near the base on the other side. Although of comparatively infrequent occurrence these intergrades furnish important links in the chain of evidence. They provide the clues enabling us to fill in the story of reduction from the
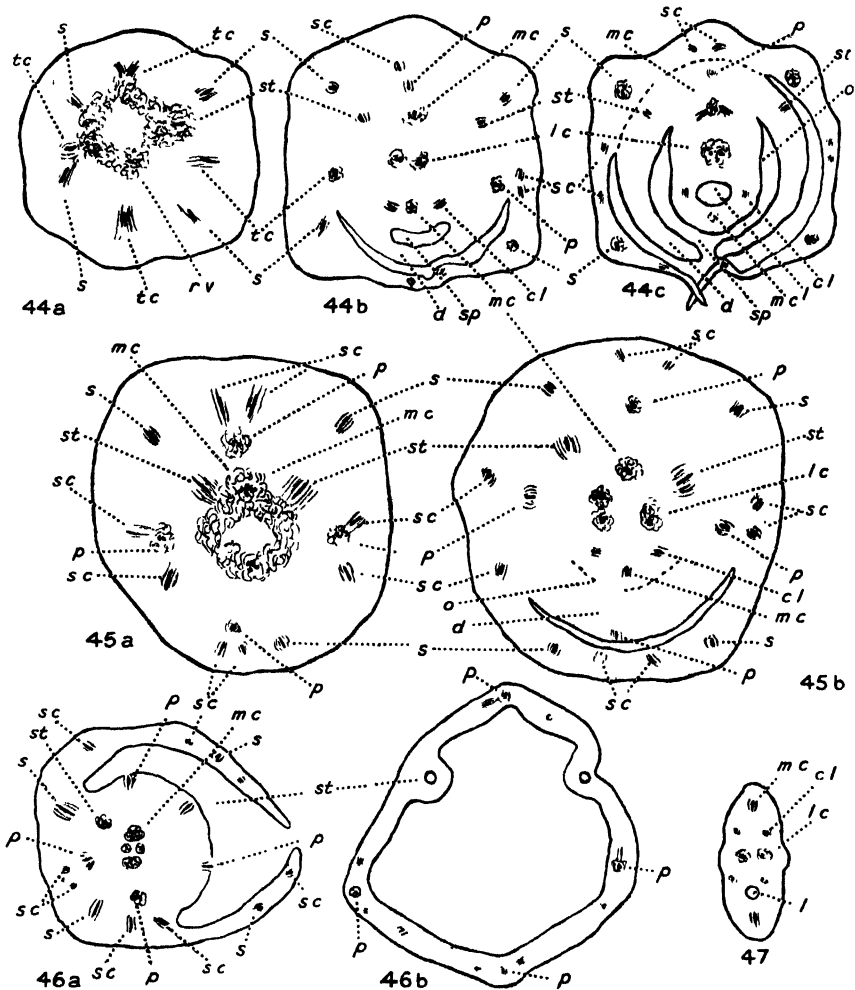
Figs. 44–47.—All from transverse sections of K 4 C 4 flowers with *one* midrib bundle in
the posterior corolla segment, taken, when in series, from below upwards. 44 *a–c*,
Veronica Anagallis L. *a*, the four diagonal sepal midrib bundles, and the four
alternate trunk cords which supply the sepal commissural marginal bundles
and the petal midribs, have left, or are in process of leaving, the central vascular
cylinder. Bifurcation of the calyx component of the anterior and posterior cords
is already indicated. The bundle for the left stamen is not yet differentiated,
but that for the one on the right is about to issue from the central cylinder. *b*, the
two antero-lateral sepals are becoming exserted, and ovary and disc are becoming
disjoined. The commissural marginals derived from the anterior trunk cord
are seen in the exserted portion of the two front sepals. The corolla component
of this cord is not seen, the anterior petal having dropped out of the space between
sepals and disc after becoming exserted. The right lateral trunk cord has under-
gone complete dissociation into petal midrib and two sepal marginals; the sepal
and petal components of the posterior cord are now disjoined, but the former

highest to the lowest grade of the 2-midribbed arrangement. This, briefly, is as follows:—Reduction from the highest duplex grade (both midribs branched bilaterally, the two systems remaining distinct) to the grade in which the two systems become continuous through the formation of a false mid-vein could obviously readily come about if either the intervening tract of non-vascular tissue became narrower, or the lowest lateral branch on the inner side of each midrib made a wider angle with the vertical. In the next stage in the downward process the portion of one of these branches extending from the midrib to the point of junction with the other branch fails to become differentiated, and ceases to be traceable. Thus there arises the 'right' or 'left' pattern described above. A similar disappearance of the basal portion of the corresponding branch of the other midrib results in the appearance of a weak median vein unconnected with either midrib. Finally, this detached vein also disappears, and the lowest grade is reached in which branching is confined to the outer side of each midrib. This appears to be the usual sequence. But in some flowers the disappearance of this mid-vein occurs before the loss of the second branch junction, which then remains as a short blunt stump. Only in two flowers on a plant of *incana* which showed other departures from type was the converse condition observed in which a transverse connection between the two midribs was present, but no upward prolongation in the form of a common mid-vein.

When we come to examine the incidence of the various meristic and vascular variations in the perianth which have been described in the foregoing pages, the striking fact which at once emerges is the high degree of instability exhibited
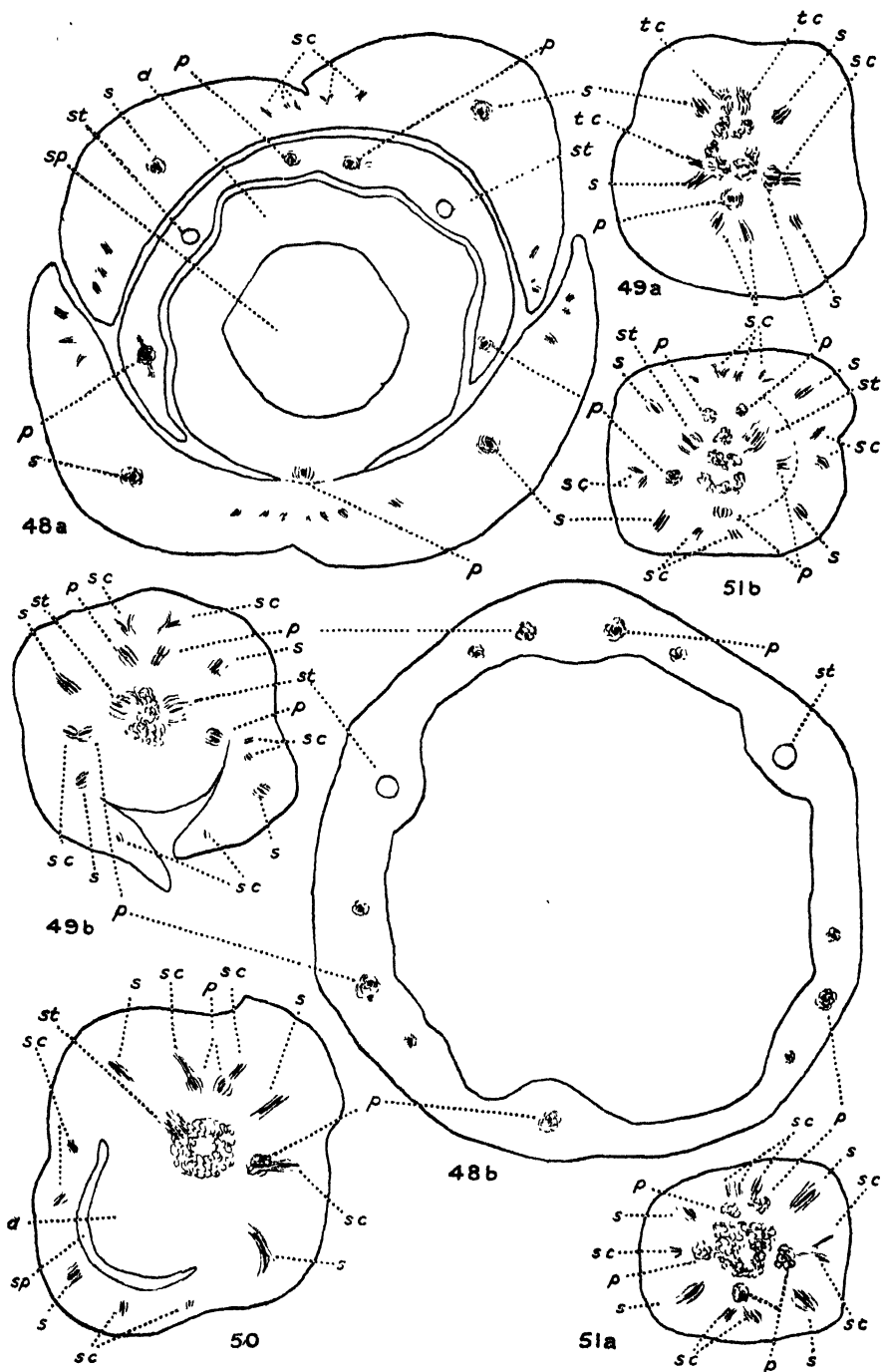
Figs. 48–51.—All from transverse sections of K 4 C 4 flowers with *two* midrib bundles in the posterior corolla segment, taken, when in series, from below upwards. 48 *a, b*, *V. speciosa* (garden form). *a*, calyx, corolla and disc. The sepals with midrib and much branched commissural lateral veins show the characteristic overlapping.

by a large number of species in respect of both types of variation. Comparatively few forms appear to have reached a condition of stability at the lowest present-day grade, viz. K 4, C 4, with one midrib in the posterior segment (indicated shortly as K 4 C 4 m 4). This will be apparent on reference to the Table facing p. 472. *Veronica Teucrium* has been described as the most variable of any known species. It may, 1 think, be added with equal truth that *Veronica* is the most variable in regard to floral structure of any known cyclic genus. In considering the *Veronica* aggregate from this point of view, it will be most convenient to treat the several sections separately.

Paederota.

Only a few flowers were examined of two species, *V. lutea* Scop. and *V. Bonarota* L., but it is clear from all accounts that in both the calyx is typically pentamerous. In both forms the corolla is furnished with five midribs, the two interstaminal bundles each branching bilaterally. In *lutea* the presence of five petals is rendered evident on inspection by the notch ordinarily occurring in the upper lip of the corolla, but in *Bonarota* this notch is usually wanting. In these species we see the two critical stages in reduction from the five-petalled corolla to one that has the appearance of being four-petalled, viz. the last stage before, and the first stage after, complete fusion of the two postero-lateral petals.

Leptandra.

The available material consisted of one clump of the white-flowered form of *V. virginica* L. The numerous spikes of flowers yielded every kind of meristic variation. Indeed, the degree of instability was so extreme that the number of exceptional flowers recorded was about double that of those showing normal development*. Although usually described as typically tetrasepalous, all

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* Owing to the variety of the deviations from normal in this material, it was found more convenient to list the variations recorded separately instead of including them in the general table facing p. 472. For the same reason this procedure was also followed in two highly unstable varieties of species belonging to the section *Pseudolysimachia*.

Figs. 52–54.—All from transverse sections of typical K 5 C 4 flowers with two midrib bundles in the posterior corolla segment, taken, when in series, from below upwards. The stages represented are similar to those shown in figs. 48–51, but differ in that a fifth (posterior) sepal is present. 52 *a, b, V. Teucrium* L. The vascular elements which give rise to the midrib and commissural marginals of the posterior sepal, the commissural marginals of the two adjacent sepals, and the two midribs of the posterior corolla segment are seen leaving the central cylinder as a single massive trunk cord which begins immediately to dissociate into its components. *b*, after dissociation is complete. 53 *a, b, c, V. loganioides* Armstr. showing similar stages. The whole of the sepal commissural component of the posterior trunk cords passes into the two postero-lateral sepals, the posterior sepal receiving only a midrib which remained unbranched. 54 *a, b, c, V. Derwentia* Andr. *a, b*, showing similar stages. The posterior sepal, as in the preceding species, receives only the midrib bundle, but develops one true lateral branch (see *b*). True lateral branching also occurs in some of the other sepals (see *a*), although commissural marginals are present. *c*, the corolla. The posterior segment with two midrib bundles showing characteristic bilateral branching.

Analysis of the records of the exceptional flowers examined in three very variable forms, not shown in the accompanying Table.

V. virginica alba. One clump.

1	C 4 m 6 (posterior and one lateral duplex) A 2.
1	C 4 m 5 A 3.
198	C 3 m 4 (posterior duplex) A 2.
70	C 3 m 5 (posterior and one lateral duplex) A 2.
2	C 3 m 4 (posterior simplex, one lateral duplex) A 2.
17	C 3 m 3 A 2.
27	C 2 m 4 (both duplex) A 2.
30	C 2 m 3 (one simplex, one duplex) A 2.
3	C 2 m 2 (both simplex) A 2.
349	

Exceptional 349
Normal (see Table) .. 161
Total 510

V. longifolia var. rosea. One clump.

1	C 7 m 7 A 1.
9	C 6 m 6 A 2.
7	C 6 m 6 A 1.
6	C 6 m 6 A 0.
10	C 5 m 6 (posterior segment duplex) A 2.
2	C 5 m 6 (one lateral segment duplex) A 2.
1	C 5 m 6 (anterior or one lateral segment duplex) A 1.
72	C 5 or C 4 with bilobed posterior segment m 5 A 2.
1	C 5 m 5 A 1 + 1 depauperated.
3	C 5 (one lateral petal duplicated) m 5 A 2.
2	C 5 (anterior petal missing, both laterals duplicated) m 5 A 1 + 1 petaloid.
1	C 5 (one petal missing, two petals duplicated) m 5 A 2.
48	C 5 m 5 A 1.
37	C 5 m 5 A 0.
1	C 4 m 6 (posterior segment and one lateral petal duplex) A 2.
2	C 4 m 5 (one lateral petal duplex) A 2.
1	C 4 m 5 A 0.
2	C 4 m 4 A 1 + 1 petaloid.
1	C 4 m 4 A 1 + 1 fused with adjacent petal.
1	C 4 m 4 A 1 + 1 depauperated.
3	C 4 m 4 A 1.
1	C 4 m 4 A 1 petaloid.
3	C 4 m 4 A 0.
1	C 3 m 4 A 2.
216	

Exceptional 216
Normal (see Table) .. 66
Total 282

V. foliosa var. exaltata. One clump.

1	C 6 m 7 A 2.
1	C 6 m 6 A 1.
2	C 5 m 5 A 2.
1	C 5 m 5 A 1 + 1 petaloid.
1	C 5 m 5 A 1 + the vascular bundle of the other.
7	C 5 m 5 A 1.
2	C 5 m 5 A 1 petaloid.
1	C 5 (anterior or one lateral duplicated) m 5 A 1.
1	C 5 m 5 A 2 G petaloid.
1	C 4 m 5 A 1.
1	C 4 m 5 (one lateral petal duplex) A 2.
15	C 4 m 4 A 2 petaloid.
37	C 4 m 4 A 1 + 1 petaloid.
2	C 4 m 4 A 1.
4	C 4 m 4 A 1 petaloid.
77	

Exceptional 77
Normal (see Table).. 65
Total 142

Figs. 55–59.—All from transverse sections of exceptional flowers. *55 a, b, V. Teucrium* var. *thracica* Velenovsky. The corolla showing ingrowth of the conjoined edges of the two petals forming the posterior segment. *a* with single superposed flap (see text-fig. 39 *a*), *b* with two flaps turned back to back (see text-fig. 39 *b*). *56–58, V. Bux-baumii* Ten. From flowers with an oligomerous corolla. *56*, from a K 4 C 3 m 4 flower. The right lateral petal and midrib are missing, the whole of the corresponding trunk cord having been used up in supplying the two sepal marginals. *57*, from a C 3 m 4 flower in which the whole right trunk cord and petal are missing. The sepal midribs show true lateral branching. (For the exceptional form of one postero-lateral sepal member, see text-fig. 40 *b*.) *58*, from a C 3 m 4 flower in which the anterior petal is missing. (For the exceptional form of one antero-lateral sepal member, see text-fig. 40 *a*.) *59 a, b, c, V. vernicosa* L. From a flower with a duplex anterior corolla segment. *a*, before, *b*, after, partial exsertion of the corolla (see also text-fig. 22). *c*, a portion of the ovary. The main bundles for the two fertile lateral carpels are not yet differentiated, although the midribs for the two median sterile carpels have turned out far enough from the central cylinder to permit of the appearance of the loculi and have formed lateral branches.

the normal flowers I examined were pentasepalous. Fischer (6) concluded from his observations that K 5 is constant in this species, but this opinion does not accord with descriptions of the plant in its North American home (see 8). The corolla in the normal flowers was typically tetrapetalous with two midrib bundles in the posterior segment, less than 7 per cent. of such flowers being recorded as simplex. Both midribs showed unilateral branching only. We here see reduction carried distinctly further than in the two preceding species, the average level in *virginica* being lower both as regards petal number and vascular development in the posterior corolla segment. It may be remarked in passing that the clump of *virginica* in question had been established in the Cambridge Botanic Garden for a long period of years.

Pseudolysimachia.

If the material investigated of *V. incana* L., *V. hybrida* L., *V. longifolia* L., *V. spicata* L. may be taken as a representative sample, then this section must rank as the most stable of all those under consideration, the several component species appearing to have reached the present-day limit of reduction*, and to have become stable at that grade (K 4 C 4 m 4). All the normal flowers recorded were, without exception, simplex (text-figs. 1, 2, 46 *a*, *b*). In three of the four species there was also complete, or almost complete, absence of departure in any form from the specific type. But in this respect *spicata* proved to be distinctly less stable than the other three, about 7 per cent. of the flowers examined showing irregularities of various kinds in the corolla (text-figs. 62 *a–e*, 63 *a*, *b*). It is noteworthy, however, that although *longifolia* type was found to be a markedly stable form, a pink-flowered variety (var. *rosea*) proved to be in the highest degree unstable (text-figs. 66, 67), with very little good pollen. A high degree of instability was also noticeable in a variety of another species included in this section, viz. *foliosa* var. *exaltata*. Unfortunately no material of the type form was available for comparison. In both these varieties the numerous spikes of flowers produced by a single clump yielded every kind of meristic variation. Abnormalities of various kinds also abounded †. In *exaltata* the number of exceptional flowers was slightly in excess of those showing normal development ; in *rosea* it was more than thrice as many. Though most of the latter resembled *longifolia* type in having a single midrib in the posterior corolla segment, a minority showed two midrib bundles.

The excessive number of aberrations recorded in *rosea* together with the character of the pollen raise the question whether these departures from type are associated with aberrations in chromosome behaviour. I am indebted to Mr. E. F. Warburg for the following information regarding the *longifolia*

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* Present-day limit, that is, as a *specific* characteristic apart from *occasional* departures from type.

† For a full analysis of the records from these two varieties, see p. 473.

Figs. 60-63.—All from transverse sections taken, when in series, from below upwards. 60 *a, b, V. satureioides* Vis. From a typical (K 5 C 4) flower. The venation scheme differs in the different sepals. The posterior sepal has commissural, the

two postero-lateral sepals true lateral, marginals. The two antero-lateral sepals are without marginal veins. 61–63, from exceptional flowers. 61 *a*, *b*, *c*, *V. hederifolia* L. From a flower with a pleiomerous corolla due to duplication of the left antero-lateral petal. 62, 63, *V. spicata* L. 62 *a–e*, from a trimerous (K 3 C 3 m 3) flower. 63 *a*, *b*, from a pentamerous (K 5 C 5 m 5) flower in which the single posterior corolla segment is replaced by two petals (reversion). Fig. 64, *V. Beccabunga* L. From a K 4 C 3 m 4 flower. The right lateral petal and midrib are missing, the corresponding trunk cord, which has not yet bifurcated, being wholly used up in supplying the two sepal marginals. [For a later stage in which this cord has already undergone bifurcation in a similar exceptional flower, see text-fig. 56.]

material from which the present data were obtained. He finds that the *n* number of chromosomes in *longifolia* type and var. *subsessilis* is 34 and 17 respectively. These numbers accord with the observations of Graze (9) on this section. Unfortunately, owing to the scarcity of good pollen, no certain statement can be made respecting *rosea*. Hence the question whether the aberrant behaviour of this individual is associated with an abnormal chromosome scheme remains at the moment unsettled.

Veronicastrum, Alsinebe, Hebe.

The sections *Veronicastrum*, *Alsinebe*, and *Hebe* offer a marked contrast to the preceding section. Though each includes one or more species which have become stable at the K 4 C 4 m 4 grade, these are probably outnumbered by those composed either of individuals producing some flowers with one midrib in the posterior corolla segment and some with two, or of individuals producing solely flowers with a 2-midribbed posterior corolla segment. The following species come into the first of the above categories :—

Veronicastrum, V. gentianoides Vahl (text-figs. 45 *a*, *b*). An extremely stable form. Out of the 250 flowers examined 249 were of the normal K 4 C 4 type ; of these 248 were simplex and only one duplex. The remaining flower had a C 5 corolla owing to an unconformable variation. [The term ' unconformable ' is here used to distinguish those meristic variations which are not reversionary and do not accord with the scheme of the original ground-plan.]

Alsinebe, V. acinifolia L., *V. glauca* Sibth. & Sm. (text-fig. 6), *V. serpyllifolia* (text-figs. 3, 23 *a*, 37), *V. Cymbalaria* Bodard ; also, probably, though the counts in these species were smaller, *V. peregrina* L., *V. syriaca* Roem. & Schult., and *V. repens* Clar. Not a single duplex flower was recorded among the normal flowers of *acinifolia* (124), *Cymbalaria* (47), *peregrina* (29), *syriaca* (29), *repens* (13), and *glauca* (184) and only three out of a total of 531 in *serpyllifolia*. Reversion, reduction, and unconformable variations were either few (never exceeding 4 per cent., see Table facing p. 472) or lacking altogether (*peregrina*). The solitary instance recorded in *Cymbalaria* was of the rare form in which a C 3 corolla arises through suppression of the posterior segment (see p. 455, footnote §).
V. hederifolia L. (text-fig. 4) appears to be slightly less stable than the preceding
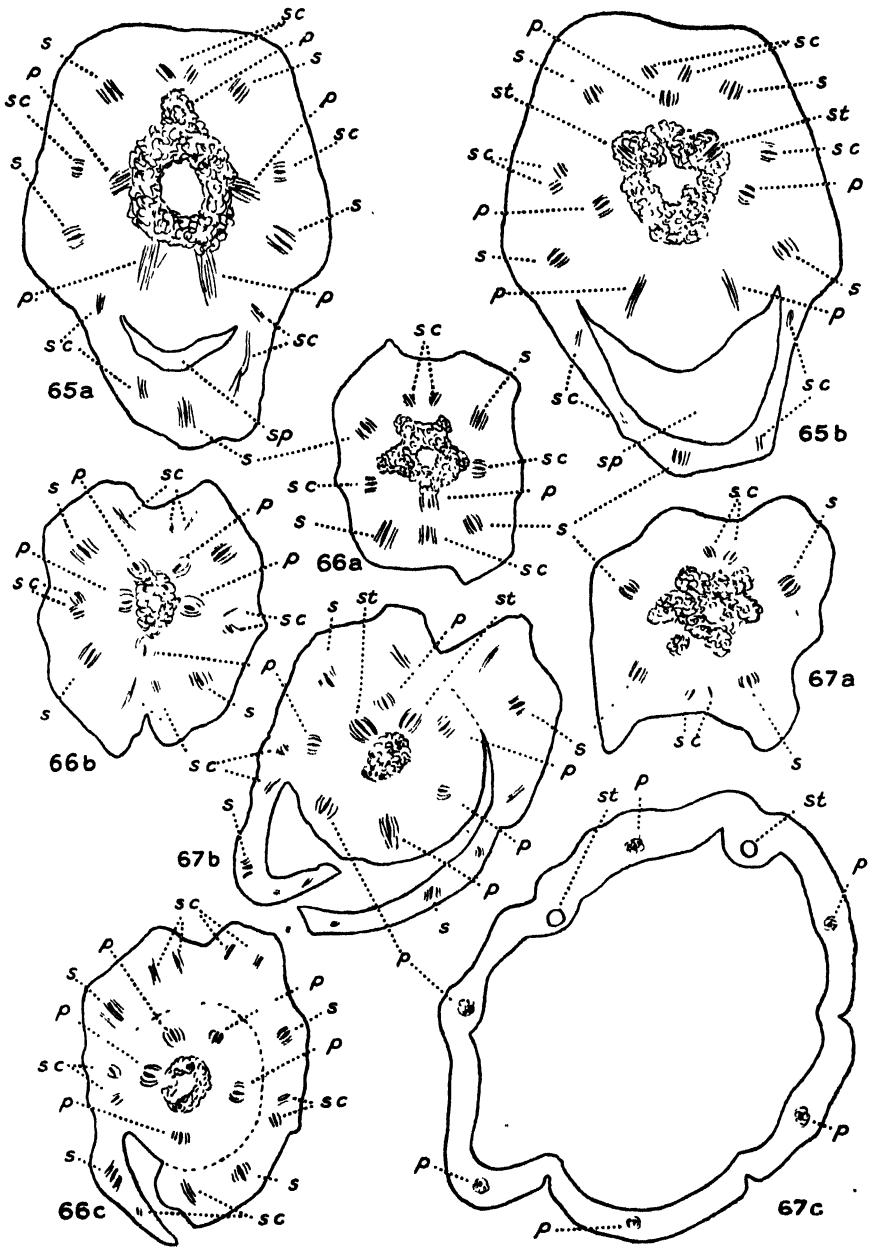
Figs. 65–67.—All from transverse sections of exceptional flowers taken, when in series, from below upwards. 65 *a, b, V. longifolia* L. From a K 5 flower with the unpaired sepal anterior. 66, 67, *V. longifolia* var. *rosea.* 66 *a–c,* from a K 4 C 5 flower lacking both stamens. 67 *a–c,* from a K 4 C 6 flower showing unconformable duplication of two petals: *a, b,* the whole flower; *c,* the corolla.

species, though whether the observed variations indicate a correspondingly higher position in the scale is, for the reason given below, uncertain. Out of a total of 290 flowers 284 were normal, and of these 260 were *typically* simplex, the other 24 flowers being recorded as duplex. Sections of one of these apparently duplex flowers revealed, however, that the two vascular systems in the back petal did not arise, as normally, on two separate radii, but that one originated as a branch from the posterior trunk cord before it became dissociated into the sepal component and the petal main bundle. The duplex appearance in this specimen is therefore probably to be attributed to premature branching of a single midrib rather than to the development of two equivalent midribs. This difference in origin cannot be recognised in the detached corolla, hence it remains uncertain whether any of the 24 flowers recorded as duplex were genuine.

The records obtained from the other category of species in these three sections will be best appreciated by reference to the Table facing p. 472. It will be seen that in those belonging to *Veronicastrum* a simplex corolla in normal C 4 flowers is quite exceptional. That 1-midribbed posterior segments should be lacking in *V. satureioides* Vis. is to be expected, since this species is typically pentasepalous (text-fig. 60 *a, b*), and, as previously explained, in these circumstances a single separate petal bundle in the midline at the back is ordinarily impracticable. This species is of particular interest from another point of view, for it appears to stand higher in the scale than any other species in any section having typically a C 4 corolla. Though complete fusion of the two postero-lateral petals must be considered to be the normal condition, the proportion of flowers showing some stage on the way to reversion to C 5 was exceptionally high. Every stage was to be found between a single posterior segment with a median notch and two fully formed segments, the total of all these grades amounting roughly to one quarter of the whole count *. This excessive number of departures from type in the direction of reversion suggests that the downgrade step from C 5 to C 4 has taken place comparatively recently. This inference is supported by other evidence. Of the 355 normal C 4 flowers recorded all without exception showed the highest grade of vascular development (two midribs, both branched bilaterally). In no other species in which a fairly large count was made was this high level maintained, lower grades always appearing in a larger or smaller percentage of flowers. In the five other species in which more than ten normal flowers were examined the variations in vascular development in the posterior corolla segment covered the range from two midribs both unilaterally branched to two midribs both branched bilaterally, the most frequent grade being that in which one midrib is branched unilaterally and the other bilaterally. As regards general type stability there were considerable differences between the members of this

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* In other species where lobing occurred only occasionally it was found possible to list these intermediate grades separately from the condition of complete segmentation (see Table facing p. 472), but in *satureioides* this was not feasible.

group. Neither conformable nor unconformable departures from type were recorded in *V. monticola* Armstr. or *V. fruticulosa* L., whereas a high proportion of exceptional flowers appeared in *V. alpina* L. (text-fig. 25), in both stocks of *V. fruticans* Jacq. (text-fig. 27), and, as mentioned above, in *V. satureioides* Vis.

In the section *Alsinebe* each of the five remaining species examined produced both simplex and duplex K 4 C 4 flowers, but otherwise showed far less uniformity than was observed among the corresponding group in *Veronicastrum*. Thus in *V. filiformis* Sm. flowers with a 1-midribbed posterior corolla segment were about twice as numerous as those with two midribs. On the other hand, in *V. Buxbaumii* Ten. and *V. polita* Fries less than 5 per cent. of the K 4 C 4 flowers were simplex, while in *V. arvensis* L. the proportion was less than one half per cent., only two being found among the 438 K 4 C 4 flowers examined.

It is not surprising to find that this diversity in regard to the proportion of normal simplex and duplex flowers is accompanied by a parallel difference in the grade of vascular development. As in the corresponding *Veronicastrum* group, the variations in development of the two vascular systems in the posterior segment usually covered the whole range of grades of branching, the one occurring most frequently in the members of the present group varying more or less directly with the frequency of occurrence of the 2-midribbed condition. Thus in *filiformis* with the lowest proportion of duplex flowers the most frequent grade is the lowest in the scale (both midribs branched unilaterally). In *arvensis*, with the highest proportion, the highest grade (both midribs bilaterally branched) greatly preponderated. In both *Buxbaumii* and *polita*, which occupy an intermediate position, the intermediate grade (one midrib branched bilaterally and one unilaterally) was by far the most abundant. · In regard to general type stability there was again a marked difference between the species in question, the percentage of exceptional flowers varying from less than 1 per cent. in *arvensis* to an extremely high proportion in *humifusa* (eleven in a total of twenty-five), although in this species the material examined was from wild plants growing in their natural habitat.

In the section *Hebe* the records suggest, as may well be the case in view of the ease with which crossing is known to take place among many of the species, that material referred to the same species was not always homogeneous ; the divergent results obtained from gatherings from different stocks of the two species *V. pinguifolia* Hook. f. and *V. Lyallii* Hook. f. being perhaps referable to this cause. A low grade type comparable in stability with those ·cited in the preceding section was found in *V. buxifolia* Benth. and in *V. gillesiana* T. Kirk. In *buxifolia* an overwhelming preponderance of the flowers examined were simplex, only four in a total of 132 normal flowers being recorded as duplex, these four all belonging to the lowest grade (both midribs branched unilaterally). In *gillesiana* the count, though much smaller, indicated similar relations. A quite exceptional feature in the latter species was the complete absence of marginal veins in the sepals (text-fig. 41 *a*). The two species

V. Hulkeana F. Muell. and *V. Olsenii* Colenso and some stocks of *V. loganioides* Armstr. stand at the opposite end of the scale, no single normal simplex flower having been observed in the individuals examined, though in another stock of *loganioides* three were recorded in a total of 131 normal flowers. Ranking as almost equally stable are *V. parviflora* var. *angustifolia* Hook. f. and one stock of *V. pinguifolia*. Only one simplex flower was recorded out of a total of 72 flowers in the former, and out of 96 in the latter plant. The other species examined occupied intermediate positions in the scale, a few showing a preponderance of simplex, the majority an excess of duplex flowers. As suggested above, the fact that different stocks of *Lyallii* and *pinguifolia* yielded opposite results in this respect raises the question whether the stocks were in each case pure bred. General stability of type was a marked characteristic of the section as a whole, and in this respect *Hebe* appears to stand higher than any of the other sections under consideration. In the majority of the species not a single exceptional flower was observed. In the *loganioides* material examined we have, however, a conspicuous exception in this respect, 20 per cent. of the flowers recorded from two stocks showing some deviation from type.

Chamaedrys.

The species included in the section *Chamaedrys* fall naturally into two groups, characterized respectively by a typically pentasepalous and a typically tetrasepalous calyx. This meristic difference in the calyx is associated with a definite, though not a corresponding, difference in the corolla, segmentation into four petals being typical of both groups. But whereas a posterior segment with a single midrib probably never occurs (for reasons explained later, p. 485) in a pentasepalous flower, a larger or smaller proportion of such segments is found in most if not all of the tetrasepalous species. The Table facing p. 472 shows that not a single simplex flower was recorded in the species usually classed as pentasepalous, except in *V. orientalis* var. *Whittalii* and *V. multifida* Jacq. Flowers of *orientalis* type were not, unfortunately, available, but those of another variety, *tenuifolia*, proved to be predominantly tetrasepalous. As it happened, no record was made of the sepal number in the 28 C 4 m 4 flowers in *Whittalii* or of the exceptional two in *multifida*, but I have little doubt, in view of all the facts, that in each case the calyx will have been tetrasepalous *.

All the species classed in *Pentasepalae* together with their derivatives showed instability in grade of branching of the midribs in the posterior corolla segment, the variations, as in the section *Alsinebe*, generally covering the whole range. The variety *Whittalii*, however, differed from the rest in this latter respect. For whereas the most frequently occurring grade in this form was that in which

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* Römpp in his recent preliminary survey of the whole genus (12) excludes *orientalis* from *Pentasepalae*. This view renders the inference drawn from the present observations on a derivative of this species all the more probable.

both midribs branch only unilaterally, the highest numbers in the other types were recorded for the form in which one midrib branched unilaterally and the other bilaterally. All the evidence thus indicates that the *orientalis* aggregate has progressed a definite stage further than the true *Pentasepalae* towards the typical form prevailing today.

Of the individuals examined belonging to typically tetrasepalous species none produced exclusively duplex flowers excepting *V. montana* L., in which only six normal flowers were available. The proportion in which simplex flowers occurred varied widely. In *V. peduncularis* M. Bieb. and *V. Chamaedrys* L., for example, such flowers amounted to less than 1 per cent. The opposite extreme, a less common condition, is seen in *V. cinerea* Boiss. & Bal., in which as many as 130 such flowers were recorded out of a total of 330.

All the species of this group showed instability as regards degree of branching of the midribs in the posterior corolla segment, and in most, as in the penta-sepalous division, the maximum count was recorded for the intermediate grade in which one midrib branches bilaterally and the other unilaterally. One species, *pirolaeformis*, however, stood higher in the scale with a maximum count for the grade in which both midribs branch bilaterally, and two, *peduncu-laris* and *filifolia*, at a lower level, the highest number being recorded for the grade in which both midribs branch unilaterally. The level of type stability is generally high, but two species afforded marked exceptions, viz. *montana* and *nivea*. In both, the count, which was small, obtained in *montana* from wild material, was made up almost equally of normal and exceptional flowers. In *prostrata*, a species included in the pentasepalous division, flowers with K 4, but in other respects typical, amounted to 15 per cent.; otherwise excep-tional flowers were in general rare, and in some species, e.g. *cinerea*, no single case was observed. The few (seven) with exceptional corollas which made their appearance in *prostrata* and *Teucrium* all came into the category of reversion to C 5. This is not surprising, seeing that all flowers in these species were duplex. Consequently the single step of segmentation of the already duplex back petal suffices to complete the reversion to C 5.

In passing, it may be noted that some material of a variety *thracica* of the pentasepalous species *Teucrium* furnished fresh evidence in corroboration of the accepted interpretation of the posterior corolla segment as being derived from the fusion of two petal members. Many flowers from a clump of this variety showed a petal-like flap of varying size superposed upon the posterior segment, giving the appearance of a small petal lying on a larger one, much as the nectary scale lies on the petal of a *Ranunculus*. Microscopic examination reveals that the flap is formed by the turning inwards together, and then away from each other, of the meeting edges of the twin petal structures which make up the posterior segment. The two ingrowths fuse along the line of junction. If the ingrowths are not too large they fuse throughout their length (text-figs. 39 *a* and 55 *a*). When they are of large size, cohesion throughout is precluded by their shape. Becoming disjoined in the upper expanded region,

both ingrowths become folded lengthwise and away from each other (text-figs. 39 *b* & 55 *b*). Thus twin flaps are formed and a condition of more or less complete reversion to C 5 *.

Labiatoides.

V. Derwentia Andr., the one species examined, proved to be a stable high grade type of the form K 5 C 4 m 5 (text-fig. 54 *a–c*). There was a total absence of flowers having only one midrib in the posterior corolla segment †, and the deviations from type, which amounted to less than 1 per cent., were reversions to the full ground-plan (K 5 C 5 m 5). As regards branching of the two midribs in the posterior corolla segment, *Derwentia* ranks with those species showing the fullest development, such as *satureioides* in *Veronicastrum*, *arvensis* in *Alsinebe*, *pirolaeformis* in *Chamaedrys*, and *Olsenii* in *Hebe*, the largest count occurring in the highest grade (both midribs branched bilaterally), and the lowest grade (both branched unilaterally) not being recorded.

Beccabunga.

Of the three species *V. aquatica* Bernh., *V. Anagallis* L., and *V. Beccabunga* L., the two former proved to be markedly stable types of the lowest grade (K 4 C 4 m 4), comparable in this respect with *glauca* and *gentianoides*. Every normal flower, except one, showed only a single midrib in the posterior corolla segment, while departures from type through reversion or reduction ranged between 2 and 3 per cent. *V. Beccabunga*, on the other hand, growing in the same spot and close beside the plants of *Anagallis*, afforded a great contrast. In K 4 C 4 flowers the 1-midribbed condition in the posterior corolla segment, though greatly preponderating, was not invariable, more than 10 per cent. of such flowers having two midrib bundles, while the proportion of departures from type through reversion, reduction, or unconformable aberrations was exceptionally high ‡. Unfortunately this plant (A) was later almost destroyed, rendering it impossible to obtain a further count the following season. A plant (B) from another source has yielded to date 69 normal and ten C 5 flowers. Of the normal flowers, 67 were simplex and two duplex

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* This curious development would appear either to be peculiar to the particular individual plant or to be dependent upon seasonal or other environmental conditions, for I have been unable to find any reference to such ingrowths in any account or figure of this form. That certain considerable differences in the environment, as, for example, between a poor dry-as-dust earth in an unwatered cold frame in springtime and the constantly moist soil in the flower bed alongside, may affect in some measure the degree of vascular development in some annual species appeared, in fact, to be established by some of the records obtained during the present investigation. But these effects, resulting in slight variations in the relative frequency of occurrence of the different grades, do not affect the validity of the general conclusions based on the present data.

† This lack, for reasons explained later, is fully to be expected (see p. 485).

‡ No full analysis was made of these exceptional flowers, since it was found that, in many instances, the inspection method would need to be supplemented by the cutting of sections at an expenditure of time which would have involved the curtailment of observations bearing more directly on the main issue.

(lowest grade). Of the ten C 5 flowers some were due to reversion and some to duplication of the anterior segment. So far as they go, these numbers confirm the conclusion that *Beccabunga* is a less stable species than *Anagallis*. Owing to the fact that Plant A was injured before any examination had been made of the chromosomes, it is not possible to state whether the aberrations in the flowers were associated with aberrations in chromosome behaviour.

PLEIOMEROUS AND OLIGOMEROUS COROLLAS.

It remains to consider the vascular relations in general of the pleiomerous and oligomerous corollas. The range of variation in the number of corolla segments (text-figs. 35 *a–d*, 27, 28, 29) is perhaps even more remarkable than the frequency with which they occur in some species. An important point that emerges at once from microscopic investigation is that duplication of the posterior segment results from a mode of development somewhat different from that involved in duplication of the other petal members. When, in a normally tetrapetalous species, there is a return in some flowers to the original pentapetalous ground-plan, this reversionary condition is associated with the development of two posterior midrib bundles accompanied by a correspondingly adjusted segmentation of the intervening non-vascular tissue.

We have seen that in the course of reduction from C 5 to C 4 the normal relation between outward form and vascular development is commonly broken, segmentation of the non-vascular tissue ceasing completely before the reduction in vein number from two to one (rendered possible by the previous disappearance of the fifth sepal and its midrib) is effected. Imperfect coordination between these two processes is also sometimes to be seen when intermediate stages occur between the C 4 m 5 grade and a typical C 5 (see text-figs. 34 *b, c*). This fact lends support to the view that such intermediate stages represent upgrade steps on the way to reversion rather than downgrade steps in the course of reduction. When the reversion is complete, segmentation is once again in perfect accord with the vascular development (text-figs. 23 *a*, 24 *a*, 26, 32, 34 *d*). The present data indicate *that the reappearance of two posterior petals in the tetrasepalous flowers of species ordinarily producing four-petalled corollas with a one-veined posterior member rarely occurs.* No such C 5 flowers were recorded in *gentianoides, incana, longifolia* (type), *hybrida*, or *glauca*. Two and three were observed in *hederifolia* and *Anagallis* respectively, and one in a plant of *spicata* which showed considerable variability in other directions. On the other hand, in tetrasepalous flowers of species ordinarily producing both C 4 m 4 and C 4 m 5 corollas such five-petalled flowers are often of quite frequent occurrence *. This combination presents no difficulty, for the two petals formed by duplication of the posterior member are not superposed upon the two postero-lateral sepals. They occupy the

* The material employed in the three forms *longifolia* var. *rosea, foliosa* var. *exaltata*, and *virginica* (white) must obviously be left out of any such comparison, as presumably some unusual disturbing factor underlies the ' wild ' results recorded from these forms.

same radii, radii proper to petals, in the tetrasepalous as in the pentasepalous flower. Moreover, in a tetrapetalous species having characteristically flowers with a duplex posterior corolla segment, the *vascular scheme required for C 5 is there already*, and the single step of segmentation at once gives an actual C 5. *It is the superposition of midrib bundles which presents a real difficulty*, hence the combination which we do not find is that of a simplex C 4 corolla with a K 5 calyx. Such superposition upon a sepal of a petal with one midrib bundle, independent in origin, would be contrary to the general principle of alternation underlying all floral arrangement. Lehmann conceives a certain mechanical difficulty when duplication of the front far outnumbers that of the back petal (11, p. 35). But this is to presume strict equivalence of the two cases.

Duplication of either the anterior or the lateral petals is not due to reversion taking place after previous reduction, but results from a certain maladjustment in the normal process of development. Such duplication is in consequence frequently, though not invariably, asymmetrical. This maladjustment consists in the extension of the bipartition, which normally is confined to the calyx component of the sepal-petal trunk cords, so that the petal component also becomes divided in two. Thus two equivalent strands are formed in place of one (text-figs. 59 a, b, 61 b, c). Each becomes the main vein of one of the two petal segments resulting from segmentation in accord with the abnormal vascular development. Such bipartition of the whole trunk cord may occur in more than one such cord in a flower. Further, such bipartition of the anterior or lateral trunk cords accompanied by corresponding segmentation may occur simultaneously with reversionary segmentation of a normally 2-veined posterior segment, hence it will be seen that the number of petal segments may be increased to as many as ten. It remains to add that complete bipartition of a trunk cord is not always accompanied by a corresponding segmentation. When this happens the corolla remains apparently four-petalled, but one or more (as the case may be) of the three front segments is then furnished with two midribs (text-figs. 22, 33 b, 35 a, d).

Oligomerous corollas usually arise through the process of reduction being carried beyond the normal (text-figs. 36 a, b, 37, 38, 56–58, 64). The most commonly occurring form is that in which the anterior trunk cord is wholly used up in providing the two commissural sepal marginals. No anterior petal and no corresponding mid-vein are then developed. One, or even both, lateral petals may also become suppressed in this way. Suppression of the posterior segment was only observed in a single instance. In the above manner it becomes possible for C 3 and C 2 corollas to occur in conjunction with a normal K 4 calyx. Exceptionally, a reduction in petal number is brought about by fusion of two neighbouring petal segments. Oligomery produced in this latter way can be distinguished from that due to suppression by the number and mode of origin of the midrib bundles. If it is a case of suppression, each surviving segment shows normal veining. If fusion between two petal lobes occurs, the resulting segment possesses an additional midrib. When it is added that

any of the numerous departures from the normal described above may happen either singly or in combination, we are better able to understand the great variety in the number of sepals, petals, and petal midribs to be found within the genus and the frequent occurrence of any one of these three kinds of variation independently of the other two. Finally, it cannot be too strongly emphasised that only by a study of the vascular anatomy is it possible to elucidate the varied nature of these meristic differences and to distinguish those which appear to have a definitely phylogenetic significance from those which are, seemingly, merely fortuitous aberrations.

The general inference to be drawn from the present data is that the whole *Veronica* aggregate, probably without exception, either has already undergone, or is still today in the course of undergoing, an identical process of floral reduction. This process consists in the transition from the highest grade, K 5 C 5 m 5, through a series of intermediate stages to the lower grade K 4 C 4 m 4, at which point reduction is arrested and stability, for the time being, again attained. The transition from K 5 to K 4 is effected in many cases, possibly in all, by a series of stages ; that from C 5 to C 4, characteristically, in a single step, while the passage from m 5 to m 4 in the corolla again takes place in stages. In each of the larger sections *Pseudolysimachia, Veronicastrum, Alsinebe, Hebe, Chamaedrys,* and also in the small section *Beccabunga,* one or more species have now apparently attained a condition of stability at the bottom of the scale, but the bulk of the species in all but the first- and the last-named sections have not yet reached this stage. Standing at a higher level in the scale they are all more or less unstable. By observation we can ascertain the range of variation and the grade within that range which occurs most frequently. But if the view put forward by R. E. Fries is correct, that in certain East African species having typically K 4 C 5 flowers C 5 is to be regarded as an original, not as a reversionary, condition, it follows that the order of the steps in reduction in the perianth is not the same in all species, this process beginning first in the calyx of some types and in the corolla of others. Apart from the very exceptional cases coming under the former head, however, it would appear that the stage reached in reduction may be taken to indicate a certain general phylogenetic relation within each section, on the supposition, which is supported by the appearances seen in reversion, that the process of downgrade reduction has followed the same course in related species. On this view such species as *gentianoides, glauca, buxifolia, aquatica,* and *Anagallis* may be supposed to have a longer pedigree behind them than the other species in the same sections which have been considered in the present account.

SUMMARY AND CONCLUSIONS.

1. New evidence is brought forward confirming the now generally accepted view that the present-day *Veronica* flower scheme K 4 C 4 A 2 G (according to the theory of carpel polymorphism) 2+2 has come about through reduction from an isomerous pentamerous ground-plan (K 5 C 5 A 5 G 5+5).

2. Reduction from K 5 to K 4 has proceeded by the disappearance gradually of the fifth posterior sepal and of the outgoing vascular bundle on that radius. Reduction from C 5 to C 4 has been brought about by the congenital fusion of the two postero-lateral petals. These two processes take place independently of one another. This is exemplified in numerous species which regularly produce K 5 C 4 flowers, and in others in which K 4 C 5 flowers are either characteristic or of occasional occurrence.

3. These processes of reduction are still in progress today, with the result that the great majority of the species are in an unstable state, the individual exhibiting considerable variations in perianth number and in the vascular ground-plan of the corolla. Viewed from this standpoint alone, apart from all vegetative characters, *Veronica* appears to be more variable than any other known cyclic genus.

4. Instability in the calyx is most frequently manifested in the form of meristic variations. These generally take the form of reversion to K 5 with segmentation and vascular development in complete accord. In other cases they are the outcome either of a further stage in reduction (K 3) or of a modification of the original ground-plan (e.g. K 5 with the unpaired sepal anterior or K 6). These latter non-reversionary variations are usually accompanied by a corresponding variation in petal orientation and number. Exceptionally, partial fusion—in other words, incomplete segmentation—may give rise to intermediate states between typical K 5 and typical K 4. In such cases segmentation and vascular development are not infrequently maladjusted.

5. Sepal marginal veins are almost invariably present and are typically commissural in origin, a trunk cord leaving the central cylinder on the radius of each petal and dissociating later into three strands—the adjacent marginal vein for each of the two neighbouring sepals and a petal midrib. When, however, through a maladjustment in development, the calyx component after becoming detached passes wholly into one of the neighbouring sepals, the other, deprived of its commissural vein, may develop a marginal vein through true lateral branching. An altogether exceptional case is that of *V. gillesiana*, in which marginal veins appear to be entirely lacking.

6. Instability in the corolla, in some form, is a characteristic feature of a high proportion of species. Occasionally it is so extreme that less than one third of the flowers in a gathering are found to show full normal development. In general, it takes the form of variations in the number of segments and of midrib bundles. These two forms of variation usually occur independently of each other when the posterior sector alone is involved ; simultaneously, and in direct relation to one another, when anterior or lateral petals are concerned.

7. The usual meristic variations in the corolla may be classed under three heads :—(*a*) Reversion from C 4 to the original ground-plan (C 5) through the re-appearance of two postero-lateral petals in place of a single posterior segment. (*b*) Further reduction from C 4 to C 3 or even to C 2 through suppression in the one case of the anterior, and in the other of both lateral

petals, or, more rarely, through fusion.   Variations under these two heads may conveniently be described as conformable, since they come within the scheme of the original ground-plan.   (c) Unconformable departures from the original ground-plan through duplication of the anterior or lateral petals or of both, thus again giving rise to C 5 or to higher numbers.

8. Since the same meristic result may be produced by conformable and by unconformable variations, a record of exceptional petal numbers is of comparatively little value unless supplemented by evidence showing whether these numbers are due to reversion, fusion, unconformable duplication, or a combination of these processes.   Critical evidence whereby these different cases may be distinguished is furnished by the vascular system.

9. Reduction from the five-petalled to the four-petalled condition through obliteration of the posterior median division, so that the whole width of the interstaminal portion of the corolla forms one entire segment, appears, ordinarily, to be effected in a single step.   Although in a few types every intermediate stage can be observed from a mere emarginate apex to the normal degree of segmentation, it is probable that these exceptional cases represent upgrade stages in reversion rather than downgrade stages in reduction.

10. The attendant but independent process of reduction from the 5-midribbed to the 4-midribbed condition takes place, on the other hand, in a series of stages. The various well-defined vascular configurations to be observed in the single posterior segment of C 4 corollas, in descending order, are as follows :—

(a) Two midrib bundles, each bilaterally branched, the two systems remaining distinct throughout.

(b) Two midrib bundles, each bilaterally branched, the two systems becoming continuous through the formation of a false mid-vein derived from the fusion of two basal lateral branches, one from each midrib.

(c) Two midrib bundles, one branched bilaterally, the other unilaterally, on the side away from the centre.   This grade being asymmetrical appears in two patterns distinguishable as ' right ' and ' left '.

(d) Two midrib bundles, both branched unilaterally, each on the side away from the centre.

(e) One midrib bundle branched bilaterally.

11. It follows from these facts that until the final stage is reached in the process of reduction from C 5 to C 4, the usual strict relation between the scheme of segmentation and the vascular ground-plan is broken.

12. It follows, further, that the single posterior segment in the *Veronica* corolla is not morphologically equivalent to the other segments except in the minority of cases in which reduction to the lowest grade in the scale is complete. The anterior and lateral petals of the normal flower are both ontogenetically and phylogenetically unit structures (simplex).   The posterior segment with two midrib bundles, though ontogenetically similarly simplex, is phylogenetically duplex.   It occurs in both penta- and tetrasepalous flowers, but the simplex condition is incompatible with K 5, unless the posterior sepal midrib arises conjoined with a neighbouring bundle.

13. In further reduction from C 4 to C 3 and C 2 by suppression, the suppressed member and midrib disappear simultaneously, hence the ordinary relation between petal number and midrib number is not disturbed. It is again upset, however, in the rarer case where C 3 results from fusion of the anterior petal with one of the lateral members. Reduction to C 3 may occur with, or without, a corresponding reduction in sepal number. When there is reduction to C 2 the calyx usually remains tetramerous.

14. Evidence that vascular development in the corolla as a whole is undergoing a general decline apart from the specific trend towards reduction of two vascular systems to one in the posterior segment is afforded by the very frequent occurrence in all the petals of isolated strands, connection with the main system being no longer traceable.

15. In all the species examined which normally produce K 5 C 4 flowers, as e.g. those belonging to the pentasepalous division of the section *Chamaedrys*, two vascular systems were found to be present in the posterior corolla segment of all flowers. This may be expected always to be so in such species, since the vascular bundle for the posterior sepal occupies the mid-line at the back, hence if further development is to be symmetrical the vascular elements which supply the posterior duplex segment of the corolla must leave the central cylinder at two points, to right and left of the middle line respectively.

16. Those species examined which normally have K 4 C 4 flowers were found, on the other hand, to fall naturally into two groups, one consisting of a few species which have reached the lowest grade in this category and have become stable at that level, producing typically flowers with only one bundle in the posterior corolla segment ; the other comprising a very much larger number which, though tending to this level, are in an unstable condition, producing in varying proportions flowers with one midrib in the posterior corolla segment and others with two.

17. Only a single C 4 species among the many examined having typically two vascular systems in the posterior corolla segment, viz. *satureioides*, proved to be in a condition of stability as regards the particular grade of vascular development in this segment. Every individual investigated of other species coming under this head showed a range of two or more of the grades described above (see paragraph 10), indicating a general trend in all such species in the direction of the replacement of the two systems by one.

18. Perianth relations characterizing species in the different sections indicate :

(a) That the two species in the New Zealand section *Pygmaea*, *V. ciliolata* and *V. pulvinaris*, with an altitude range of 5500 to 6500 feet, and the two tropical East African species of the section *Veronicastrum* recently discovered by R. E. Fries, *V. keniensis* and *V. aberdarica*, with a range from 3700 to 3800 m. above sea level, all having characteristically K 5 C 5 flowers, are primitive types, since in no other species in which C 5 appears undoubtedly to result from reversion is this condition constant and regularly associated with K 5. This conclusion arrived at independently is in accordance with the view put

forward by R. E. Fries in his account of the two above-mentioned African species, in which he states that C 5 in these species must be regarded as an original character.

(b) That for similar reasons the two species *V. lutea* and *V. Bonarota* in the section *Paederota* are also to be regarded as early forms, the latter species with the posterior corolla segment characteristically entire but occasionally notched representing one step further in the direction of reduction than the former, in which this segment is occasionally entire but generally notched.

(c) That in the white-flowered form of the species *virginica* in the section *Leptandra* reduction has reached a further stage, both calyx and corolla varying (according to the accounts of systematists) between the pentamerous and tetramerous condition, the number of midrib bundles in the corolla being, however, almost always five.

(d) That the section *Pseudolysimachia*, which, so far as appears, includes only species which have become stable at the level which today represents the end term in the scale of reduction (K 4 C 4 with one vascular system in the posterior segment), is the furthest removed as regards floral construction from the ancestral type.

(e) That in the section *Beccabunga* two species (*Anagallis* and *aquatica*) have also undergone reduction to the K 4 C 4 m 4 grade and have become stable at this level, while another species (*Beccabunga*) has reached a point but little short of the same stage.

(f) That the large sections *Veronicastrum, Alsinebe, Chamaedrys,* and *Hebe* are not, like the preceding sections, homogeneous groups. All four sections comprise both species of the lowest grade (K 4 C 4 with m 4) and higher grade species (K 4 C 4 with m 5–4). Further, *Veronicastrum* and *Chamaedrys* include also some K 5 C 4 species, and *Veronicastrum* some K 5 C 5 species. The K 4 C 4 m 4 species are stable as regards both segmentation and midrib number, the two features being in accord. The K 4 C 4 m 5–4 species, though stable in regard to segmentation, are unstable as regards both midrib number and the bilateral or unilateral branching, when five midribs are present, of the two in the posterior corolla segment. The records indicate a general downgrade trend in all the species examined, the degree of instability being slight in the highest grade and increasing as reduction proceeds until the K 4 C 4 m 4 stage is established.

(g) That the pentasepalous species *Derwentia* in the section *Labiatoides* like the pentasepalous species in *Chamaedrys* probably produces only flowers with a duplex posterior corolla segment and like certain other species showing a high grade of vascular development in this segment is a markedly stable form.

19. Reversion from C 4 to C 5 appears to be most frequent in those species which still typically retain two midrib bundles in the single posterior segment of the normal C 4 flowers. In such types the necessary vascular framework in all or many of the flowers already exists, hence only the further single step

of segmentation is needed. If a pentamerous corolla appears in a species ordinarily having only one midrib bundle in the single posterior segment, this condition is generally due to a different cause, viz. duplication of the anterior or of the lateral petals, i.e. to pleiomery arising from unconformable aberrations as distinct from reversion.

20. In the normal partially gamopetalous corolla of any *Veronica* the processes of growth which result in a maximum development of the corolla on the one set of radii (or sectors) and a minimum development on the alternate set are so perfectly coordinated that a prolongation down the tube of the segmentation which defines the free lobes would also separate the vascular system of any petal from that of its neighbour. But when pleiomery occurs through unconformable aberrations, or even through reversion, these growth relations are occasionally imperfectly adjusted, with the result that the radius on which growth is retarded and segmentation occurs does not correspond exactly with the dividing line between the vascular system of the petal on one side and that of the petal on the other side, but traverses a portion of the system of the one petal which has extended into the sector of the other petal.

21. The pleiomerous corolla arising through duplication of the anterior or lateral petals (unconformable aberrations) is associated with a definite maladjustment in the break-up of the trunk cords which furnish the sepal marginals and petal midribs. Bipartition, which normally is confined to the sepal component of the cord, here extends to the petal component. In this way two bundles arise which become the midribs of the two petals formed by duplication.

22. No generalization can be made with regard to the occurrence of pleiomery due to unconformable aberrations. Such aberrations lie outside the general evolutionary trend in the direction of reduction in progress throughout the whole *Veronica* aggregate. They appear to be entirely erratic in their incidence and to be of common occurrence in certain species (or individuals) irrespective of whether these species (or individuals) show stability or instability as regards the vascular development of the posterior corolla segment.

23. Oligomerous corollas may arise (*a*) through an alteration in the ground-plan affecting both perianth whorls, or through suppression of one or two of the ordinary petals without corresponding alteration in the calyx. In this latter case no petal component is detached from the trunk cord on the radius of the missing member, the whole of the cord being appropriated to the sepal marginals. Or, (*b*) more rarely, by fusion, usually of the anterior petal with one of the lateral members. Here the resulting duplex segment shows two midrib bundles.

24. So far as can be judged from the small number of species which have been examined in regard to chromosome number, conformable meristic variations in the corolla cannot be correlated with particular chromosome configurations, but it may be that frequency of unconformable variations in the corolla will be found to be associated with aberrations in chromosome behaviour.

25. Ground-colour patterns in the corolla, when present, are associated with

specific areas. They retain these fixed positions irrespective of the number of segments or of the pattern of the vascular scheme in particular segments.

26. Colour patterns superposed upon the ground colours, when present, are associated with the vascular system and differ in design in particular segments according as one or two midrib bundles are present. If well defined, the superposed pattern enables one to determine merely by inspection whether one or two midribs are present in any segment.

27. Reversion in the androecium from A 2 to A 3 or A 4 appears to be wholly erratic in its incidence. It occurs comparatively rarely, either without other departure from the normal or in conjunction with duplication of the anterior or one of the lateral petals.

28. The fact that in some species the two carpel bundles in the lateral plane become differentiated later in time and at a higher level than the two median carpel bundles affords confirmatory evidence that the gynoecium consists of two pairs of carpels.

29. Reversion from a dimerous to a trimerous ground-plan in the gynoecium also appears to be quite erratic in occurrence. No additional departure from type was observed in the few flowers in which this variation was recorded.

30. Exceptionally, the styles may be disjoined, the ovary being surmounted by two normally and equally developed filaments.

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The Water Relations of the Plant Cell. By ELIZABETH C. M. ERNEST,
Ph.D. (Lond.). (Communicated by Professor V. H. BLACKMAN, F.R.S.,
F.L.S.)

(With 2 Text-figures)

[Read 2 March 1933]

THE whole surface of a land plant is continually losing water at a greater
or less rate, and there is a continuous flow of water through the plant from the
roots in the soil to the aerial parts. The root hairs absorb the water from the
soil solution, and it passes across the cortical cells into the vascular system
and thus into the tracheids in the leaves. From these tracheids the water
passes through mesophyll cells to stomatal cavities and so into the atmosphere.
An understanding of the water relations of the plant requires a study, therefore,
of the properties and behaviour of the cell ; each one of the many mechanisms
of the cell must be studied before we can hope to understand the sum of the
behaviour of the groups of many different but coordinated cells in the plant
body.

The plant consists of cell wall, protoplasm, and cell sap. The protoplasm
is semi-permeable, permitting the passage of water but preventing to some
greater or less extent the passage of dissolved substances. An osmotic
pressure is produced by the sugars and salts in the sap, and this pressure
tends to draw water into the cell and so to increase the cell volume, and
therefore to distend the cell wall. The cell wall is extensible only to a limited
degree, and therefore it tends to prevent an increase in the volume of the cell.
Water reaches the cell vacuole through the cell wall, which is fully permeable,
and which is believed to offer little if any resistance to the passage of water
or dissolved substances, and through the protoplasm which is semi-permeable
and which probably offers some resistance to the passage of water. The
water is held in the vacuole by the ' effective ' osmotic pressure or suction
pressure.

The effective osmotic pressure is usually less than the full osmotic pressure
of the contents of the vacuole. The suction pressure, for instance, of a
mesophyll cell from a leaf of *Iris* is about ten atmospheres. Therefore the
osmotic pressure is greater than or equal to ten atmospheres. If the cell
is immersed in water to reduce the suction pressure to zero and then trans-
ferred to a sugar solution of one atmosphere osmotic pressure, water is with-
drawn from the cell. Therefore water in this example is held within the
cell by a force less than the osmotic pressure of the cell contents.

The amount by which the effective osmotic pressure or suction pressure is less than the osmotic pressure of the cell solution depends on the distension of the cell wall. Very few data exist concerning the elasticity or the extensibility of the cell wall, but this would seem to be one of the most important characters of the cell from the aspect of water relations. The degree of extension from the plasmolyzed to the saturated state varies considerably from species to species, and from tissue to tissue. Tables I & II give the least area of one surface in square μ, and the extensibility expressed as percentage increase in area from the plasmolyzed to the saturated state of ten mesophyll cells from the leaves of a number of species of *Iris*. The preparations

TABLE I.—Iris variegata *var.* aurea. *Extensibility of cell wall.*

Area.	Turgor extension.
sq. μ.	
1490	8
1570	7
1250	8
1500	6
1190	3
830	9
1300	9
1400	12
1000	8
1790	7

TABLE II.—Iris. *Extensibility of the cell wall in different species.*
Each figure represents the average of ten cells.

	Area.	Turgor extension.
	sq. μ.	
Iris asiatica	1670	8
—— Delaveyi	275	10
—— flavescens	1600	10
—— foetidissima	1660	8
—— olbiensis	2480	7
—— pallida	1610	7
—— variegata var. aurea	1330	8
—— versicolor	950	10

were made by inserting a sharp scalpel in the surface of the leaf and tearing away a strip of superficial tissue. In this way intact mesophyll cells were obtained attached to the epidermis. The strip of tissue was immersed in . distilled water for one hour to allow the cells to attain to their greatest volume, and then mounted in distilled water and placed under a microscope with camera lucida and a group of ten cells drawn. The water was then replaced by a plasmolyzing solution of cane sugar and the same group of cells was redrawn when just plasmolyzed. The surface-area is the most reliable measurement, because of the many sources of error in any estimation of the volume of

irregular plant cells. The least surface-area is obtained at incipient plasmo-
lysis. If the protoplast contracts further the cell frequently shows an apparent
increase in surface-area owing to the collapse of the side-walls. Pressure of
the cover-slip on the preparation is best prevented by use of a slight excess
of mounting liquid; this is preferable to using cover-slip supports. The
precaution is a very necessary one as external pressure may in a similar way
cause an apparent increase in the surface-area of the cell.

TEXT-FIG. 1.
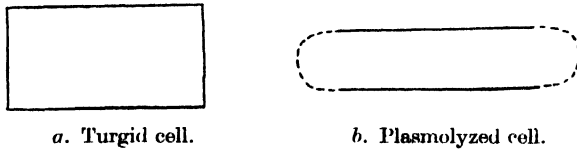
a. Turgid cell. *b.* Plasmolyzed cell.
The cell contents contract and the walls collapse.

An explanation of apparent increase in surface-area of plasmolyzed cells.

TEXT-FIG. 2.
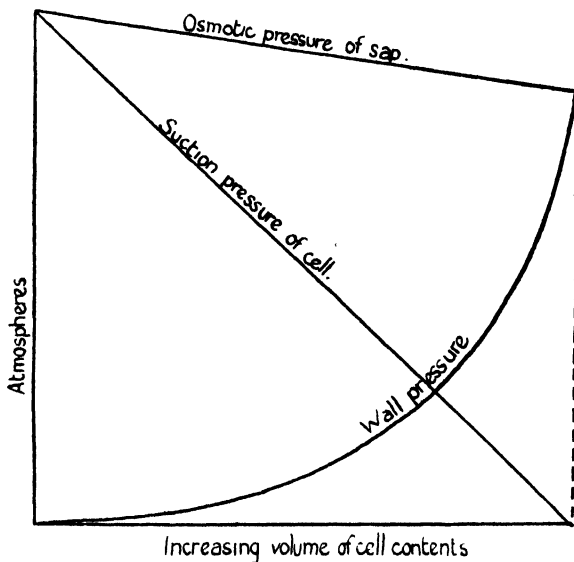
The relation between osmotic, wall, and suction pressures and the volume
of cell contents in a cell with a partially extensible wall.

It will be seen from the tables that the surface-area of the cells and the
extensibility of the cell wall vary considerably from one species of *Iris* to
another. In *Iris Delaveyi*, for instance, the extremely small cells of surface-
area of about 275 sq. μ show a ' turgor extension ' of 10, while cells of *Iris
olbiensis* have an area of some 2,500 sq. μ and a ' turgor extension ' of 7.

The extensibility of the cell wall varies considerably from one tissue to another in the same leaf. The epidermis is usually rigid. In a hybrid *Iris* (*I. Forrestii* × *Bulleyana*, Table III), from the leaves of which cells of several tissues could be excerpted, the more or less regular mesophyll cells had an average surface-area of 800 sq. μ and a turgor extension of 13. Close to the veins, however, were two series of elongated cells, the outer having an average area of 850 sq. μ and turgor extension of 10, while the cells nearer to the tracheids were nearly four times as large and showed an almost negligible change in area.

TABLE III.—Iris Forrestii × Bulleyana. *Turgor extension of the cell wall in different types of mesophyll cell.*

Rounded cells.		Small elongated cells.		Large elongated cells.	
Area.	Turgor extension.	Area.	Turgor extension.	Area.	Turgor extension.
sq. μ.		sq. μ.		sq. μ.	
790	16	1010	16	3660	3
830	6	560	7	4570	1
910	9	560	13	2330	0
890	11	850	10	2700	2
700	29	920	7	2350	0
770	10	1160	4	3000	3
660	11	1070	9	4410	3
790	8	550	14	3040	0
870	19	710	10	3300	6
830	10	1130	8	3170	0
Average. 800	13	852	10	3253	1·8

TABLE IV.—*Extensibility of the cell wall in some herbaceous plants. Each figure=average of ten cells.*

	Area.		
	sq. μ.		
Cochlearia anglica	2430	....	17
—— *officinalis*..................	1405	....	10
Isatis Boisserianum	1168	....	15
—— *glauca*	1040	....	16
—— *tinctoria*..................	745	....	25
Viola tricolor	1360	....	7

Table IV gives the surface-area and extensibility of the mesophyll cells attached to the lower epidermis of the leaves of six herbaceous plants, each figure representing the average of ten cells, and in Table V are given the areas of ten mesophyll cells and ten epidermal cells of *Ceropegia Woodsii*. The cells of the latter plant show no extensibility whatever.

The water exchange of a cell is determined by its suction pressure, and this is the resultant of the opposing osmotic and wall pressures, and therefore the suction pressure depends, apart from the available water, on the osmotic

content of the cell sap and on the extensibility of the cell wall. As Thoday (2) has shown diagrammatically, a small decrease in the osmotic pressure of the sap induced by entry of water into a cell can cause an increase in wall pressure and, consequently, a considerable fall in suction pressure. The relation between these quantities (the osmotic, wall, and suction pressures of the cell and the volume of the cell contents) depends, however, on the degree of distension and on the extensibility of the cell wall. Text-fig. 2 shows this relation in an extensible wall, and this is probably typical of mesophyll cells of herbaceous plants, where the wall pressure increases as the volume of the protoplast and vacuole increases, and the suction pressure can be of any value between zero and the osmotic pressure of the sap. In some cells, however, the wall is rigid. This condition is known to occur in the walls of submerged plants and in *Ceropegia Woodsii*, and I have found it in the large cells of *Opuntia*. I believe the condition to be typical of xerophytes. When the cell is saturated the wall pressure is at a maximum and the suction pressure

TABLE V.—Ceropegia Woodsii. *The surface-area of the epidermal and and mesophyll cells. Area in sq. μ.*

Epidermis.	Mesophyll.
800	4350
560	4970
900	1650
960	2810
950	3330
1530	2720
630	3000
1130	3460
470	2790
400	3750
Average 830	3283

is equal to zero. When the cell contents lose water the surface-area of the wall remains unchanged, and therefore, the wall pressure falls to zero immediately, and the suction pressure becomes equal to the full osmotic pressure of the cell sap.

The importance of these mechanisms to the plant is obvious. The extensible wall is found in mesophytes whose water supply is normally fairly constant, and the balance between the osmotic and wall pressures is maintained, sometimes at least, at a remarkably constant value. The plants with rigid cell walls would seem, however, to be able to adapt themselves to extreme conditions of water supply.

In the saturated condition, and while loss and gain of water can proceed at the same rate, cells having either extensible or non-extensible walls behave in the same way, and a maximum evaporation takes place from the wall-surface, since, if the suction pressure of the cell is zero, the vapour pressure

at the cell-surface is that over water. When, however, loss of water exceeds by a little the intake of water, the extensible wall of the one type of cell contracts and the increase in suction pressure is greater than the increase in osmotic pressure, but there is still a positive wall pressure, so that the suction pressure is less than the osmotic pressure by the amount of the wall pressure; for instance, if the contents of the fully extended cell have an osmotic pressure of twenty atmospheres, the wall pressure is also twenty atmospheres and the suction pressure is zero, but if loss of a small quantity of water concentrates the cell solution and raises its osmotic pressure to twenty-one atmospheres, and if the wall pressure decreases by two atmospheres, then the suction pressure of the cell has increased from zero to three atmospheres. If, however, the cell has a non-extensible wall, a similar slight loss of water causes the wall pressure instantaneously to fall to zero and the suction pressure to rise to twenty atmospheres. By this mechanism of the non-extensible wall a maximum flow of water through the cells occurs in conditions of plentiful water-supply, and yet immediately this water-supply falls off the extreme water-holding and water-absorbing powers of the cell are called into play, and the cell is thus enabled to maintain itself through extremely different external conditions.

The suction pressure of the cells of a leaf in which the cell walls are extensible is measured on cells in the ' strip ' preparations already described, and never on cells in sections for the reasons given in an earlier paper (1). The strip is immersed in paraffin to prevent any exchange of water with the exterior and cut into several wedge-shaped pieces. One of these is mounted in paraffin and a group of cells is selected, towards the tapering end of the wedge for convenience, and the outline of the cells of the group is drawn under a camera lucida. The paraffin is then replaced by a cane-sugar solution, and after the necessary interval the area of the cells is compared with the outline drawing. This procedure is repeated until the sugar solution of the same osmotic pressure as the suction pressure of the cells is found, in which the area of the cells neither increases nor decreases. The suction pressure gradients believed on *a priori* grounds to be maintained within the intact plant necessarily disappear when any tissue or organ is removed from the plant, and the measured suction pressure therefore seldom, if ever, is that exerted by the same cell when within the plant. A mean value only can be obtained, which is a modification of the original suction pressure of the cell, and is contributed to by all the cells isolated with and at the same time as the cell under consideration. Therefore, in general, several values of the suction pressure of the cells of any convenient tissue may be obtained, according as the tissue is isolated from the intact plant or is taken from some excised portion of the plant. The differences in the suction-pressure values of material obtained by these techniques are at present the only evidence of the existence within the plant of those gradients in suction pressure which are believed to control and to be controlled by the movement of water through the cells lying between the conducting elements and the transpiring superficial cells.

The values of suction pressure obtained by these different techniques vary from one another only by small amounts and the value of the suction pressure of the cells of leaves is maintained remarkably constant, at least in the two plants studied in the course of this work, as is shown in Table VI. The mean suction pressure of cells of excised leaves of *Iris* and *Saxifraga umbrosa* was measured at intervals of two hours through a period of twenty-four hours. The variation in suction pressure was extremely slight, being only a change

TABLE VI.

Iris florentina. ⎱ *Equilibrium suction pressure of all the cells of the leaf*
Saxifraga umbrosa. ⎰ *through twenty-four hours.*

Time.	Suction pressure, cane sugar (M.).	
	Iris.	*Saxifraga.*
3 p.m.	0·398	—
5	0·398	—
7	0·398	0·325
9	0·395	0·330–5
11	0·393	0·330–5
1 a.m.	0·393	0·330–5
3	0·393	0·330–5
7	0·393	0·335–40
9	0·393	0·335–40
11	0·393	0·335
1 p.m.	0·395–6	0·335
3	0·398	0·335–40

TABLE VII.—Iris florentina. *The equilibrium suction pressure of the cells of the leaf, in leaves from four plants.*

			Suction pressure, cane sugar (M.).
1st plant.	Leaf	1	0·390
	,,	2	0·390
	,,	3	0·390
2nd plant.	,,	4	0·390
	,,	5	0·390–0·391
	,,	6	0·391–0·392
3rd plant.	,,	7	0·390
	,,	8	0·391
4th plant.	,,	9	0·390–0·391
	,,	10	0·390–0·391

from 10·89 atm. to 11·05 atm. in *Iris* and from 8·85 atm. to less than 9·29 atm. in *Saxifraga*, through a day and a night.

The mean suction pressure of the cells of each leaf of a plant is also remarkably constant in *Iris*. Table VII gives the mean suction pressure of cells from four plants, ten leaves in all, of *Iris florentina* : and the maximum variation is seen to be equal to a change in concentration of 0·002 M. cane-sugar solution, cells from five of the leaves having the same suction pressure of

0·390 M and those from the remaining five leaves having suction pressure not exceeding 0·392 M.

A convenient leaf structure which permits the ' stripping ' off of the epidermis and a greater or smaller number of attached mesophyll cells, though not of universal occurrence is fortunately to be found in a number of plants, and Table VIII gives the mean suction pressure of cells of leaves from species of *Barbarea, Cochlearia, Helleborus, Isatis,* and *Viola.*

Ecologists have frequently attempted to relate some physiological feature of the plant to the habitat, and have often selected osmotic pressure as the most probable indicator of the relation between the plant and the humidity

TABLE VIII.—*Equilibrium suction pressure of cells of leaves from several herbaceous plants.*

	Suction pressure, cane sugar (M.).
Barbarea vulgare	0·30–0·31
Cochlearia anglica	0·31–0·32
Helleborus lividus	0·29–0·30
Isatis Boisserianum	0·31–0·32
—— *glauca*	0·30–0·31
—— *tinctoria*	0·30–0 31
Viola tricolor	0·25–0·26

conditions of the environment, but variations in the osmotic pressure of the cell probably result more nearly from differences in internal structure and from varied processes of metabolism than from environmental factors. Further, there is as yet no satisfactory method of measuring osmotic pressure, since the plasmolysis method gives only an approximation to this value, and the expressed sap used for cryoscopic determinations of osmotic pressure is derived of necessity from a large number of cells and from several tissues and includes the contents of both the protoplasm and the vacuole. Suction pressure, however, is the property by which the cell maintains and controls the movement of water within the plant and the intake and loss of water by the plant, and, therefore, it seems to be a factor of importance probably not less than that of the osmotic pressure in the water exchange of the plant cell.

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Peucedanum and Steganotaenia in Tropical Africa.

By Cecil Norman, F.L.S.

[Read 1 March 1934]

It is hoped that the following brief account of Peucedanum and Steganotaenia in Tropical Africa may be useful in bringing together and accounting for the species described up to date.

Engler's account of Peucedanum in 'Pflanzenwelt Afrikas', iii, 2, p. 283 (1921), though far from complete, is the most comprehensive and recent hitherto published, and I have followed it fairly closely both as to limits and sub-division in so far as it applies to the region under review, the only important difference being that I have restored Hochstetter's Steganotaenia (regarded by Engler as a section) to generic rank. Besides this I have omitted the section Argutiserrata Engler. Of the three species from our region included in this section, two have proved to belong to other genera, and the third quite unlike the other two seems to me to be better placed in the section Crenato-serrata. (For the fourth species, from Madagascar, with which we are not concerned, the section may be retained.) Finally, two new sections are instituted for two species with very marked characteristics which Engler had not seen.

The classification is based mainly on the leaf characters, though not entirely, and I think it will be found that, on the whole, the plants group themselves more naturally under these characters than they would do by using the fruit. An additional advantage in the leaf characters lies in the fact that plants are usually collected with leaves, whereas fruit is too often either entirely wanting or so immature as to be misleading, for it is essential that if fruit is to be used it should be mature. As with species from other parts of the world the fruit in the Tropical African species shows a good deal of variation. The two most obvious variations occur in the dorsal ribs and the breadth of the wing. The ribs are either filiform and inconspicuous, or thick and prominent in varying degrees, while the wing may be either very narrow (± 1 mm.) or relatively very broad (± 3 mm.). But whatever the variations in other respects may be, in all species of Peucedanum as here understood two characters are invariably present, viz. (i) a stylopodium, (ii) the vittae or oil-tubes. In Steganotaenia both these characters are absent, and their absence seems to me amply to warrant generic recognition. Their combined absence is very rare, if not unique in the family. Moreover, and perhaps even more important, neither of the species included in the genus has the appearance of Peucedanum. Both flower without leaves, and S. araliacea is a shrub or tree that may attain to a height of 30 feet (Welwitsch).

Thirty-one species of *Peucedanum* are dealt with in this paper. Several, and not only the later ones, are still imperfectly known. No doubt, as more material becomes available, modifications and adjustments of the views here expressed will be necessary.

Two species, *P. serratum* and *P. angustisectum*, were originally described under *Lefebvrea* †, presumably on account of their long narrow leaf-segments. But surely the distinction between *Lefebvrea* and *Peucedanum*, such as it is, must be looked for in the fruit and not in the leaves.

As for the distribution of the species, it is not my intention to say much. They are scattered about over the whole region wherever the altitude is not below about 3000 feet, being probably entirely absent in the low-lying coastal districts and in heavy forest.

Several are true mountain plants occurring only at the higher elevations of the mountains, e.g. *P. Kerstenii, P. abyssinicum, P. Scottianum,* and *P. Winkleri*, while others are confined to the plateaux or lower foot-hills, e.g. *P. aculeolatum, P. heracleoides, P. Claessensii,* and *P. Eylesii*, to name but a few.

No district or region seems to be particularly favoured, though they are no doubt most numerous in mountainous or hilly country. Details as to localities can be gleaned from the specimens cited.

None of the species is known to occur in South Africa. Here the bulk of the species occur far to the south and are not at all nearly related to those of the tropics. But an exception must be made for two species from the Transvaal, viz. *P. venosum* Burtt Davy, which certainly seems near to *P. Grantii*, and *P. megalismontanum* Sond., which is much like the close-growing form of *P. Harmsianum* (Fries 1031), though certainly not identical. In N. Africa the species are very few and again quite distinct.

In conclusion, I now offer my grateful thanks to all those—too many to mention by name—who have lent me specimens and answered my questions.

' *Key to Genera.*

Perennial herbs flowering with the leaves. Basal leaves compound, very rarely simple. Fruit orbicular, oval or elliptic, or pyriform, always surrounded by a wing which may be broad or narrow, but does not enclose the stylopodium and is not thickened at the margins. Dorsal ribs filiform or rather thick, and then appearing close together. *Stylopodium and vittae always present*, the latter extending the full length of the seed .... PEUCEDANUM.

Tree (or shrub) or perennial herb from woody rootstock. Leaves (in *S. araliacea*) pinnate. Fruit ovate or obovate, margin winged, the dorsal ribs elevated below the disc, filiform on the back of the seed. *Stylopodium and vittae absent* .... STEGANOTAENIA.

PEUCEDANUM Linn. Sp. Pl. p. 245 (1753) et
Gen. Plant. ed. 5, p. 116 (1754).

Key to Sections.

A. Basal leaves compound.
  * Stem and rays smooth, glabrous or not.
    i. Wing of fruit not exceeding 1 mm. broad.
      Leaves bi- or tri-pinnatisect, $\pm$20–30 cm. long, oblong-lanceolate, ultimate segments linear, not exceeding 3 mm. broad .... I. CERVARIA.
    ii. Wing of fruit exceeding 1 mm. broad (except probably *P. Zenkeri* and *P. Matirollii*).
      Leaves as in Section *Cervaria*, but deltoid in outline; glabrous. Fruiting pedicels very long, 25–30 mm., hair-like .... II. CAPILLIPES.
      Leaves very large, bi- or tri-pinnatisect, 50–60 cm. long, very finely divided ultimate segments linear acute $\pm$4 mm. long from subulate to $\pm$1 mm. broad; plant more or less densely and softly pilose .... III. KERSTENIANA.
      Leaves (bi- or tri-) pinnate or pinnatisect, leaflets or segments very variable from linear to broadly ovate, margins crenate or serrate .... [SERRATA. IV. CRENATO-
      Leaves bi-pinnate, leaflets broadly ovate, deeply lobed, margins long-toothed............................. V. DENTATA.
      Leaves bi-pinnate, leaflets lanceolate acute, margins quite entire .... VI. RUNSSORICA.
  ** Stem and rays densely muriculate .... VII. MURICULATA.
B. Basal leaves simple .... VIII. SIMPLICIFOLIA.

I. Section *Cervaria* Drude in Pflanzenfam. iii, 8, p. 236

Leaves bi- or tri-pinnatisect, $\pm$20–30 cm. long, oblong-lanceolate in outline, ultimate segments linear, not exceeding 3 mm. broad.
  a. Fruit elliptic or elliptic-lanceolate.
    Leaves † $\pm$18 cm. long, ultimate segments acute, 5–10 × $\pm$2 mm., fruit 11 × 4 mm. .... 1. *P. abyssinicum.*
    Leaves $\pm$7 cm. long, ultimate segments 10 × 1 mm.; fruit 5 × 3 mm. .... 2. *P. Friesiorum.*
    Leaves $\pm$20–30 cm. long, ultimate segments mucronate 20–30 × 2 mm.; fruit ? .... 3. *P. aberdarense.*
    Leaves $\pm$20 cm. long, hispidulo-hirsute; ultimate segments acute, 5 × 1 mm.; fruit 7 × 4 mm.............. 4. *P. Englerianum.*
  b. Fruit pyriform; leaves $\pm$20 cm. long; ultimate segments 17 × 3 mm.; fruit 13 × 8 mm. .... 5. *P. Harmsianum.*

II. Section *Capillipes* Norman.

Leaves as in Sect. *Cervaria*, but deltoid in outline; fruiting pedicels very long, 25–30 mm., hair-like; fruit pyriform, 10 × 7 mm. .... 6. *P. Gossweileri.*

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† Throughout basal leaves unless otherwise stated, and measurements always excluding the petiole,

III. Section *Kersteniana* Engler in Pflanzenwelt Afrikas, iii, 2, p. 826.

Leaves very large, up to 50–60 cm. long; bi- or tri-pinnati-
sect, very finely divided, ultimate segments subulate,
±4 mm. long, whole plant more or less densely and softly
pilose .... 7. *P. Kerstenii.*

IV. Section *Crenato-serrata* Engler (*Argutiserrata* Engler, pro parte), loc. cit. p. 825.

Leaves pinnate or bi- or tri-pinnate, or pinnatisect, generally
large; leaflets or segments crenate or serrate, very variable in
shape from linear to broadly ovate. Fruit pyriform elliptic
or orbicular.

    a. Leaflets or segments linear or lanceolate.

Leaves (stem) pinnate or bi-pinnate, ±20 cm. long; glabrous;
leaflets linear, ±10×1 cm., acuminate, recalling those of
Lefebvrea Stuhlmannii, but very strongly serrate and not
triplinerved; fruit narrow-oblong, 12×6 mm. .... 8. *P. serratum.*

Leaves (stem) ternato-pinnate, ±10 cm. long; glabrous; leaflets
narrow lanceolate acute, membranous, serrulate, ±6×·5 cm.;
fruit oval, 6×4 mm. .... 9. *P. angustisectum.*

Leaves bi-pinnate, ±25 cm. long; glabrous; leaflets narrow
lanceolate acute, often lobed, remotely serrate, ±3·5–6×
·6–·8 cm. .... 10. *P. Eylesii.*

Leaves bi-pinnate, ±36 cm. long; glabrous; leaflets narrow
lanceolate, often lobed, strongly and very regularly serrate,
distinctly glaucous beneath up to 7×1·5 cm.; fruit
elliptic-oblong, 10×6 .... 11. *P. monticola.*

Leaves bi-pinnate, ±36 cm. long; sparsely pubescent, glaucous;
leaflets broadly lanceolate or ovate, irregularly inciso-serrate,
±8×2 cm., fruit elliptic-oblong .... 12. *P. Petitianum.*

Leaves bi-pinnatisect, ±30 cm. long; rather densely pubescent,
not glaucous; segments lanceolate acute to ovate, serrate,
often lobed, grey pallid beneath, ±3×1·5 cm.; fruiting
pedicels very thick and stiff; fruit subpyriform or elliptic-
oblong, ±15×8 mm.................................. 13. *P. Claessensii.*

    b. Leaflets or segments narrow-ovate or oblong-acute.

Leaves (stem) tri-pinnate, ±20 cm. long; glabrous; leaflets
narrow-ovate or oblong-obtuse, often incised, distantly
crenate, ±1–2×·5–1 cm.; petiole and rhachides flat,
slightly winged; fruit oval-oblong, ±10×7 mm. .... 14. *P. Scottianum.*

Leaves bi-pinnatisect, ±40 cm. long; glabrous; segments ovate
or oblong, acute, lobulate crenate, ±3×1 cm.; fruit oblong,
11×7 mm.. 15. *P. Winkleri.*

Leaves as in *P. Winkleri;* fruit sub-orbicular, 8×6 mm., deeply
cordate at the base .... 16. *P. Linderi.*

Leaves ±60 cm. long; densely grey-hairy; segments ob-
tuse-lobulate, coarsely crenate, with obtuse-mucronulate
teeth .... 17 *P. elgonense.*

c. Leaflets ovate.
    i. Stem and petioles covered with prickles .... 18. *P. aculeolatum.*
    ii. Stem and petioles without prickles.

Leaves bi-pinnatisect, $\pm$22 cm. long; glabrous except the
    minutely scabridulous nerves; segments ovate or rhombic,
    incised up to 2·5×2 cm., coarsely crenate; fruit elliptic-
    oblong .... 19. *P. doctoris.*
Leaves bi-pinnate, $\pm$10 cm. long; leaflets elliptic-ovate
    acuminate, strongly serrate up to 7×2·5 cm.; fruit narrow
    elliptic-oblong, 10×5 mm. .... 20. *P. Grantii.*
Leaves ternate or bi-ternate, $\pm$12 cm. long; stem pubescent;
    leaflets acuminate up to 8×5 cm., strongly serrate; fruit   [*manianum.*
    ovate .... 21. *P. Wilde-*
Leaves (stem) pinnate, $\pm$8 cm. long; glabrous, leaflets ovate-
    acuminate, serrate up to 4×2 cm.; fruit (immature) narrow-
    elliptic .... 22. *P. Zenkeri.*
Leaves (stem) pinnate; petiole and nerves beneath with a few
    scaly hairs; leaflets glabrous, often trilobed, obovate, obtuse,
    dentate-lobulate, $\pm$3×1·5 cm.; fruit acutely lanceolate,
    cordate at base, $\pm$8×3 mm. .... 23. *P. Mattirollii.*
Leaves bi-pinnate, $\pm$16 cm. long; glabrous, leaflets triangular-
    ovate, 1·5–4 cm. long, margins remotely crenate, fruit ovate,
    $\pm$10×6 mm. .... 24. *P. madense.*
Leaves bi-pinnatisect, $\pm$10 cm. long; glabrous; segments
    variable from broadly ovate to narrow oblong acute, deeply
    toothed, up to 2·5×1·5 cm.; fruit narrow elliptic-oblong,
    $\pm$10×5 mm. .... 25. *P. nyassicum.*
Leaves bi-pinnatifid, $\pm$8 cm. long; pubescent; segments ovate-
    acute, distantly serrate up to 10×4 cm. .... 26. *P. Volkensii.*

V. Section *Dentata* Engler, loc. cit. p. 825.

Leaves bi-pinnate, $\pm$20 cm. long; glabrous; leaflets broadly
    ovate, deeply three-lobed, margins irregularly long-toothed;
    fruit oval, 7×4 mm. .... 27. *P. cordatum.*

VI. Section *Runssorica* Engler, loc. cit. p. 824.

Leaves (stem) bi-pinnate; glabrous; leaflets mostly tri-lobed,
    lanceolate sharply acute, margins quite entire; fruit ovate,
    $\pm$10×8 mm. .... 28. *P. runssoricum.*

VII. Section *Muriculata* Engler, loc. cit. p. 825.

Rays and top of stem densely muriculate, especially when young.
    Involucres and involucels narrow-linear, inconspicuous,
    $\pm$1 mm. broad .... 29. *P. muriculatum.*
Involucres and involucels linear-lanceolate, very conspicuous,
    $\pm$3 mm. broad .... 30. *P. heracleoides.*

VIII. Section *Simplicifolia* Norman.

Basal leaves simple, oblong-acute, $\pm$5×2 cm., margins entire;
    lower stem leaves lyrately pinnatifid; stem villous when
    young .... 31. *P. valerianifolium.*

The following abbreviations refer to the Herbaria at the places indicated :—

B.= Berlin.
BM.= British Museum.
Bx.= Brussels.
K.= Kew.
T.= Tervueren.

1. PEUCEDANUM ABYSSINICUM Vatke in Linnaea, xl, p. 187 (1876) ; Wolff in Notizbl. Bot. Gart. Berlin, ix (1927), fig. 15 A–C. *P. silaifolium* Hiern in Fl. Trop. Afr. iii, p. 20 (1877) ; Engler, Hochgebirg. Fl. Trop. Afr. p. 321 (1892).

Abyssinia : Gaffat, 8,200 ft., *Schimper* 1147 (type).   BM., K.

A glabrous plant up to nearly 4 ft. high.   Known only from Abyssinia, and I believe only from Schimper's specimens.

2. P. FRIESIORUM Wolff in Notizbl. Bot. Gart. Berlin, ix, p. 1119 (1927), fig. 15 F–G.

Kenya : in higher bamboo region on a grassy slope, 2,800 m., *R. & Th. Fries* 1301 (type) at Upsala.

Very close to *P. abyssinicum*, but a smaller plant with much smaller fruits.

3. P. ABERDARENSE Wolff, loc. cit. fig. 16 A–B.

Kenya : Mt. Aberdare, Sattima ; in swamp about 3,000 m., *R. & Th. Fries*, 2345 ; 2390 *a* ; 2666 (all Upsala).

4. P. ENGLERIANA Wolff, loc. cit. p. 1122, fig. 16 C–D.

Kenya : Mt. Aberdare, Sattima ; in grassy meadow 3,000 m., *R. & Th. Fries*, 2390 ; Kinangop, in grassy meadow 3,000 ft., *R. & Th. Fries* 2694 (both at Upsala).

Differs from all the three preceding species, in being ' hispidulo-hirsute ' (*Wolff*).   Except for this character it is indistinguishable from *P. abyssinicum*.

5. P. HARMSIANUM Wolff, loc. cit. p. 1121, fig. 15 D–E.

Kenya : Cole's Mill about 2,000 m., *R. & Th. Fries* 1031 ; 296 (both at Upsala).

Differs from all the preceding species in the pyriform fruit.   Its position here is doubtful.

6. P. GOSSWEILERI Norman in Journ. Bot. 1922, p. 120.

Angola : in woods on the margins of the river Lunga, *Gossweiler* 3011 (type BM.) ; right bank of Luassinga in open woods, 2715 (BM.).

A most distinct species, with leaves somewhat recalling those of *P. abys-sinicum*, though much larger, but chiefly remarkable for the very long, slender, spreading, hair-like pedicels, unique in the Tropical African species.   The rays of the terminal umbel are also very long and slender up to 12 cm.

7. P. KERSTENII Engler, Bot. Jahrb. xix. Beibl. 47, p. 43 (1894) ; Pflanzen-welt Ost-Afr. p. 299 (1895) ; *Anthriscus dissectus* C. H. Wright in Johnston's Uganda Protectorate, i, p. 326 (1902), pro parte. *P. Mildbraedii* Wolff in Engl. Bot. Jahrb. xlviii, p. 279 (1912).

Tanganyika Terr.: Kilimanjaro, 2,700 m., *Kersten* in von der Decken's Expedit (type B.); 3,600 m., *Volkens* 1180 (BM.); Ruwenzori, 11,000 ft., *Scott Elliot* 7878; 12,000 ft., *Wollaston*; Buamba, 11,500 ft., *Misses Godman* 320; Kichuchu 9800; *Misses Godman* 307 (all BM.); *Dawe* 598 (K.). Belgian Congo: Butagu, *Bequaert* 3866; Lanuzi, *Bequaert* 4699 (both Bx,); *Mildbraed* 2583 (type of *P. Mildbraedii*; B.). Muhavura Mt., 12,000 ft., *Burtt* (K.), *Humbert* (T.); Mikeno Volcano, *Humbert* 8058 (T.). 9,000 ft., *Burtt* (K.). *Scaetta* 1578 (T. & BM.). Gahinga Volcano, 11,000 ft.–13,000 ft., *Burtt* 2873 (K.). Kenya: Mt. Elgon; 13,500 ft., *Dummer*, below Jackson's Summit, *Liebenberg* 1641; *Lugard* 429 (all K.). Mt. Kenya: 9,000 ft., *Miss Napier* 696 (K.); *R. & Th. Fries*, 1237 (Upsala, Bx.).

One of the best-marked species; a stout but not very tall plant characterized by the large, very finely divided leaves softly and densely pilose.

P. Mildbraedii was separated as being less densely pilose and with broader ultimate leaf segments. The view here taken is that such variations are only what may be expected in any species.

8. P. SERRATUM, comb. nov. *Lefeburia serrata* Wolff in Notizblatt. Bot. Gart. Berlin, viii, p. 231 (1922).

Uganda : Kitish region at the foot of Mount Elgon, south side in grassland, *G. Lindblom*, s. n. (type in Riksmuseum, Stockholm).

The leaves of this species bear a slight superficial resemblance to those of *Lefebvrea Stuhlmannii* Engler, but they are much more deeply and closely serrate and the venation is very different. The fruit (quite ripe) is unmistakably that of *Peucedanum* as here understood.

9. P. ANGUSTISECTUM (Engler), comb. nov. *Lefeburia angustisecta* Engler, Pflanzenwelt Afrikas, iii, 2, p. 829 (1921): Hutchinson & Dalziel in Flor. W. Trop. Africa, i, p. 523 (1927), as regards *Preuss* 969 only.

Cameroons Mountain : *Preuss* 969; *Mildbraed* 10,925; *Maitland* 819; 1282 (all K.).

This plant, remarkable for its narrow thin leaflets, and known only from the Cameroon Mountain, does not seem to be nearly allied to any other. Mildbraed's specimen with ripe fruit, which Hutchinson and Dalziel had not seen, proves that it is not a *Lefebvrea*. I have assumed that Hutchinson's description and reference to *Preuss* 696 sufficiently fix its identity, since that specimen was sent out named from Berlin and was presumably the plant that Engler had in mind. His original and only reference to it consists of eleven words.

10. P. EYLESII Norman in Journ. Bot. 1932, p. 138.

S. Rhodesia : Macheke, 5,000 ft., *Eyles* 2006 (type K.); Rusapi, *Hislop* 2211 (K.).

'An erect herb, 5–6 ft. high, with yellow flowers' (*Eyles*).

In spite of its narrow leaflets this species bears no resemblance to, and cannot

be considered as a near ally of the preceding. It is, moreover, an inhabitant of the plateaux and not of the high mountains.

Allied to *P. doctoris.*

11. P. MONTICOLA Norman in Plant. Bequaert. iv, 3, p. 354 (err. " *monticolum* "), 1928.

Belgian Congo : Ruwenzori, on the banks of the river Butagu, *Bequaert* 3829 (type Bx.).

Evidently allied to *P. Petitianum* A. Rich., but, except that it is sometimes minutely scabridulous on the nerves, quite glabrous, and the serrations on the leaves perfectly regular. The umbel rays on the type are very few and short.

12. P. PETITIANUM A. Rich. Tentamen Flor. Abyssin. i, p. 327 (1847) ; Vatke in Linnaea, xl, p. 187 (1876), *nec* Hiern in Fl. Trop. Afr. iii, p. 20 (1877) ; *nec* Engler in Pflanzenwelt Ost-Afr. C. p. 299 (1895) ; *nec* Hutch. & Dalz. in Fl. W. Trop. Afr. i, p. 523 (1927). *P. altum* Hiern, F. T. A. loc. cit.

Abyssinia : Ouedgerate, *A. Petit* in Herb. Paris (type). Gaffat, *Schimper* 1214 (BM., K.), type of *P. altum* Hiern.

A tall glaucous plant, finely but distinctly pubescent (noticeably on the leaf sheaths), which appears to be confined to the mountains of Abyssinia.

It has been much misunderstood, *P. Winkleri* Wolff, having been generally taken for it, but, thanks to the kindness of Dr. Humbert, Director of the Paris Herbarium, I have had a portion of the type on loan, which has made identification possible.

13. P. CLAESSENSII Norman in Plant. Bequaert. iv, 3, p. 352 (1928).

Belgian Congo : Djoka (SSE. of Stanleyville), *Claessens* 1409 (type Bx.). Nyasaland, *Buchanan* 87 (BM.) ; top of Zomba, *Buchanan* 211 (K.).

A tall plant, 4–6 ft. high (according to Buchanan), whose affinities are with *P. Petitianum.* It is densely pubescent when young, and is remarkable for its thick stiff rays and pedicels. The very large fruit has a remarkably small disc and stylopodium.

14. P. SCOTTIANUM Engler, Pflanzenw. Afrikas, iii, 2, p. 826.

Herba perennis, glabra, caule caniculato, sympodialiter ramosa. *Folia* (caulina inferiora ?) ±4-jugata, tripinnata ; lamina ambitu deltoidea, ±20 cm. longa, rhachibus primi et secundi ordinis et petiolo usque 14 cm. longo anguste alatis ; foliola sessilia, anguste oblonga, obtusa utrinque pallide viridia, margine grosse crenata, crenulis mucronatis, vel incisa, 1·5–2×·5–1 cm. *Umbellae* pauciradiatae ; radii rigidiusculi, 1·5–3 cm. longi ; pedicelli erecti, inaequilongi, fructiferi ±6 mm. *Involucri* et involucell. phylla 0 vel minuta. *Flores* polygami. *Petala* purpurea, minima. *Fructus* oblongus, 10×7 mm., basi subcordatus, alis ±2 mm. latis nitidis saepius purpureo-tinctis. *Stylopodium* parvum, conicum, basi undulatum. *Styli* delapsi.

Uganda : Ruwenzori, 9,600 ft., *Scott Elliot* 7631 (type B.). BM., K.

Seems to be nearest to *P. runssoricum* Engler, with which the fruit agrees very well, but differing in the obtuse crenate leaflets †.

† See 19. *P. doctoris,* footnote.

As this plant has never been discussed in literature since Engler's very inadequate original reference to it, I have thought it desirable to give the above description.

15. P. WINKLERI Wolff in Bot. Jahrb. xlviii, p. 278 (1912). *P. Petitianum* Auct. non A. Richard. *P. Petitianum* var. *kilimanscharica* Engl. Bot. Jahrb. xix, Beibl. 47, p. 46.

Fernando Po : Clarence Peak, 9,000 ft., *Mann* 608 (K.). Abyssinia, *Schimper* 871 (K.). Cameroons : Buea, *Preuss* 966 (B.) ; Bambuttu berg, *Ledermann* 1768 (B.). Tanganyika Terr. : Marangu, *Volkens* 290 (BM.) ; *Winkler* 3862 (type B.). Kenya : Mt. Kenya, near the Forest station, *R. & Th. Fries* 608 (Upsala).

A tall and rather variable species and the one that has been generally mistaken for *P. Petitianum* A. Rich. It occurs on all the high mountains except the Ruwenzori group, where its place seems to be taken by the next species.

16. P. LINDERI Norman, sp. n.

Herba alta, glabrata, caule ramoso. *Folia* basalia ? 4-jugata, jugis inter se remotis, bi- vel tripinnatisecta ; lamina ambitu deltoidea, ±27 cm. longa cum petiolo ±20 cm. longo, basi anguste vaginante suffulta ; segmenta ultima acuta, subtus pallida, eleganter reticulata eis *Peucedani Winkleri* Wolff vix dissimilia nisi magis tenuiter serrata. *Folia caulina* superiora pinnata, segmentis incisis obtusis 1·5–2·5×1 cm. petiolo omnino vaginante. *Umbellae* ±15 radiatae ; radii inaequilongi, 1·5–4 cm. *Involucri phylla* 0, involucell. pauca tenuissima acuta. *Flores* polygami, masculis in centro umbellul. dispositis brevissime pedicellatis. *Petala* delapsa, ex coll. parva flava. *Fructus* ambitu suborbicularis basi profunde emarginatus vel cordatus usque 8×7 mm. *Mericarpia* dorso ob juga primaria crassa sub-convexa ;. alae paene 3 mm. latae nitidae. *Stylopodium* conicum prominens basi dilatatum undulatum. *Vittae* intrajugalis 1, commissurales 2 sub pericarpium incrassatum latentes ; semen dorso 4-sulcatum.

Hab. Belgian Congo : Mt. Niragongo, *Linder* 2080 (type K.) ; Nyamlagira Volcano, *Lebrun* 4908 (T., BM.).

Known only so far from the volcanos to the south of the Ruwenzori *massif*, though a plant collected by Wollaston on Ruwenzori may be identical. But without fruit it is impossible to be certain.

It is impossible to believe that this species is not very closely allied to *P. Winkleri*. The leaves are almost indistinguishable, yet the fruit is so different that it might be held to require a separate Section in the genus. The commissural vittae are plainly visible on a cross-section of the mericarp.

17. P. ELGONENSE Wolff in Notizbl. Bot. Gart. Berlin, viii, p. 230 (1922)
Kenya : Mt. Kenya, *R. & Th. Fries*, 780, 1393, 2259 (Upsala). Mt. Elgon, *G. Lindblom*, s. n. (type in Riksmuseum, Stockholm).
Closely allied to *P. Winkleri*. It is much larger in all its parts, the leaf-

segments more obtuse, and densely pubescent when young, becoming less so as the plant matures. The fruit is that of *P. Winkleri*.

18. P. ACULEOLATUM Engler, Bot. Jahrb. xix, Beibl. 47, p. 43 (1895) ; Pflanzenwelt Ost-Afr. C. p. 300.

Tanganyika Terr. : Kilimanjaro, *Haarer* 643 (K.) ; Marangu, *Volkens* 718 (BM., K.). Kenya : Limaru, *Scheffler* 277 (BM., K.), *Dummer* 1520 (BM.), *Snowdon* 601 (K.). Mt. Elgon, *Snowden* 453 (K.) ; *Dummer* 3505 (K.).

Distinguished from all other African species by the ' prickles ' on the stem and petioles. They appear to decrease with age or perhaps get rubbed off, as they seem to consist in a disintegration and hardening of the outer skin rather than to be true thorns or prickles. The nerves beneath are rather stiffly hispid.

19. P. DOCTORIS Norman in Plant. Bequaert. iv, 3, p. 352 (1928).

Belgian Congo : Tshiterunge, on old lava, *Bequaert* 5977 (type Bx.) ; Tanganyika Terr. ; Mbulu Distr., *Burtt* 1249 (K., BM.).

Quite glabrous, except for the minutely scabridulous nerves. A puzzling species ; the stem-leaves on the type-specimen arising less than two inches from the base are totally unlike the true basal leaves. In the latter the leaflets are more or less ovate-obtuse ; in the stem-leaves they are long narrow linear-lanceolate, deeply and evenly serrate †.

20. P. GRANTII Kingston ex Oliver in Trans. Linn. Soc. xxix, p. 79 (1873), t. 43 ; Hiern, F. T. A. iii, p. 21.

Uganda : banks of Unyoro, *Speke and Grant* 581 (type K.) ; village of N'Langara, White Nile, *Petherick* (K.).

Oliver (loc. cit.) wrongly identified this species with Schimper's plant (236) from Abyssinia, which is not a *Peucedanum*, but *Erythroselinum atropurpureum* (Steud. ex A. Rich) Chiov., and of which I have had excellent material from Eritrea kindly sent by Dr. Negri of Florence.

21. P. WILDEMANIANUM Norman in Cont. Flor. Katanga Suppl. ii, p. 99 (1929).

Belgian Congo : Katanga ; Munama, *Quarré* 1110 (type Bx.) ; Kufubu, *Quarré* 1552 (Bx.).

Evidently nearly related to and may prove inseparable from *P. Grantii*, but more material is needed before the point can be decided.

22. P. ZENKERI Engler ex Wolff in Bot. Jahrb. lvii, p. 231 (1921).

Cameroons : Sauaga river, *Zenker* 1471 (type B.). BM., K.

A little-known plant, all the material of which is poor and imperfect. Its position is quite uncertain, but it seems to belong to the genus.

23. P. MATTIROLLII Chiov. in Nuov. Giorn. Bot. Ital. no. 3 (1929), p. 365.

S. Abyssinia : Arussi, Bocagi in the Galamo valley ; *Chiovenda* 61 (type Turin).

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† Since the above was written, it has become evident that this species is very close to *P. Scottianum*, though for the present the two are kept distinct.

Another little-known, but certainly distinct, species. The type is almost leafless and the fruit immature, but nearly approaches that of *P. abyssinicum*. True position uncertain.

24. P. MADENSE Norman, sp. n.

Herba glaberrima alta, caule terete purpurascente valde ramoso. *Folia* 4-jugata, bi-pinnata, petiolo $\pm$14 cm. longo suffulta ; lamina ambitu late deltoidea, $\pm$16 cm. longa, pinnis inter se remotis longe petiolulatis ; foliolis 1·5–4 cm. longis triangularibus-ovatis, profunde trisectis, margine remote crenatis. *Umbellae* $\pm$8-radiatae, radiis inaequilongis 1·5–4 cm. longis, pedicellis fructiferis 4–6. *Flores* polygami, delapsi. *Bracteae* involucri et involucellorum 0 vel deciduae. *Fructus* ovatus, $\pm$10 $\times$ 6 mm. *Stylopodium* conicum, parvum ; styli brevissimi.

N. Nigeria : Mada Hills, Wana, *Hepburn* 93 (type K.).

Perhaps allied to *P. Winkleri*, though quite distinct. It is a good deal like some forms of the European *P. alsaticum* Linn.—presumably a coincidence. The specimen, though a good one, is badly pressed, and so almost impossible to describe adequately.

25. P. NYASSICUM Wolff in Engler Bot. Jahrb. xlviii, p. 282 (1912).

Nyasaland ; Mt. Milangi, *Whyte*, s. n. (type B.), BM., K.

This well-marked species can always be recognized by the peculiar leaves of the top of the stem, consisting of a wide sheath crowned by long linear pinnae sharply and regularly toothed. Known only from Whyte's specimens. Wolff had not seen the fruit, which is mature on the BM. specimen.

26. P. VOLKENSII Engler, Bot. Jahrb. xix, Beibl. 47, p. 43 (1894) ; Pflanzenwelt Ost-Afr. C. p. 299.

Tanganyika Terr. : Kilimanjaro, *Volkens* 1364 (type B.), *H. H. Johnston* 149 (K.).

The type-specimen (with which Johnston's specimen exactly conforms) is a stout finely pubescent plant with very large sheaths to the upper stem-leaves. It has well-developed involucral bracts of both kinds and thick rays. There is no sign of fruit on either specimen, but its inclusion seems justified owing to its slight resemblance to *P. nyassicum* in leaf-characters.

27. P. CORDATUM Balf. fil. in Proc. Roy. Soc. Edinb. xi. p. 514 (1882).

Socotra, *Balfour* 290 (BM.).

The only species recorded from the island, and with no obvious affinity with any known species from the tropics of the African continent. The fruit is remarkable for the long and conspicuous stylopodium.

28. P. RUNSSORICUM Engler, Bot. Jahrb. xix, Beibl. 47, p. 44 ; Pflanzenwelt Ost-Afr. C. p. 300.

Ruwenzori, *Stuhlmann*, s. n. (type B.), *Scott Elliot* 7866 (BM.), *Lebrun* 4522 (T., BM.), *Fishlock and Hancock* 47 (K.), *Bequaert* 3636 (Bx.). Niragongo volcano, *Burtt* 3178 (K.) ; Mt. Mahasura, *Snowden* 1553 (K.).

A very well-marked species, unlike any other.

29. P. MURICULATUM Welw. ex Hiern in Welwitsch, Cat. Afr. Plants, 1, ii, p. 429 (1898).

Angola : Huilla, between Mumpulla and Nene, *Welwitsch* 2520 (type), 2521 (both BM.). Belgian Congo : Katanga, Lukofu, *Verdick* 321 (Bx.).

As in the following closely allied species the papillae with which the stem and rays are densely covered become far less obvious as the plant matures.

30. P. HERACLEOIDES Baker in Kew Bull. 1897, p. 268. *P. kingaense* Engler, Bot. Jahrb. xxx, p. 368 (1901). *P. Bequaertii* Norman in Plant. Bequaert. 4, ii, p. 306 (1927).

Tanganyika Terr. : Nyika plateau, *Whyte* 224 (type K.). Ukinga mountains, *Goetze* 955 (type of *P. kingaense*, B.), BM. Angola : Libolo, *Dawe* 332 (K.). Belgian Congo : Elisabethville, *Bequaert* 359 (type of *P. Bequaertii* Bx.), *Homblé* 224 ; valley of the Kapiri, *Homblé* 1240 ; Kafubu, *Quarré* 1572, *Robyns* 1545 ; River Lubichi, *Capt. Eeschamps*, s. n. ; Tumbutumbu, *de Witte* 162 (BM.), road of the Lumbubathi, *Robyns* 1638 (all Bx.).

P. Bequaertii was originally separated from *P. heracleoides* on account of its small round fruit. A closer examination of Whyte's type-specimen has convinced me that this distinction is not sound. Even on that specimen there is noticeable variation. It is unfortunate that of all the specimens examined from the Belgian Congo only *Bequaert* 359 has any fruit at all. But in a mere matter of size variations are certain to occur. The leaves are extremely variable.

31. P. VALERIANIFOLIUM Baker in Kew Bull. 1897, p. 269 (*P. valerianae-folium*).

Nyasaland : Mount Zomba, 4,000–6,000 ft., *Whyte*, s. n. (type K.).

Unique and distinct in having the basal leaves simple and quite entire. It will be interesting to know if this is always so. It was described as glabrous, and is so in the upper parts, but the lower part of the stem, at least in the young state, is rather densely villous. Believed to be known only from Whyte's specimens.

STEGANOTAENIA Hochst. in Flora, xxviii (1844), Beil. 4.

Tree or shrub ; disc flat or concave	1. *S. araliacea.*
Perennial herb ; disc hollow or cup-shaped	2. *S. Hockii.*

1. STEGANOTAENIA ARALIACEA Hochst. loc. cit. *Peucedanum araliaceum* Benth. & Hook. f. ex Vatke in Linnaea, xl, p. 188 (1876) ; Hiern in Flor. Trop. Afr. iii. p. 21 ; Engler in Pflanzenwelt Ost-Afr. C. p. 300 ; *Peucedanum fraxini-folium* Hiern, loc. cit. p. 22 ; Engler, Hochgebirg Flora, 320. *P. araliaceum* var. *fraxinifolium* Engler, Pflanzenwelt Ost-Afr. C. p. 300 ; *P. fraxinifolium* var. *haemanthum* Welw. ex Hiern in Welw. Cat. Afr. Plants, 1, ii, p. 429.

Abyssinia, *Schimper* 923. Eritraea, *Pappi* 195. Uganda, *Bagshawe* 334. Kenya : Rift Valley, N'gong-Narok Rd., *Miss Napier* 776 (K.). Tanganyika Terr. : Tendaguru, *Migeod* 270 ; Nyasaland, *Buchanan* 318. Rhodesia :

Bulawayo, *Eyles* 1251 ; Victoria Falls, *Misses Godman* 203 ; Melsetter District, *Swynnerton* 176. Angola : Zenza do Golungo, *Welwitsch* 2518 ; Commondai, *Gossweiler* 5108 (all BM.). Belgian Congo : Elisabethville, *Homblé* 277 (Bx.) ; Lukofu, *Verdick* 176 (Bx.). Cameroons, *Mildbraed* 929 (K.) ; N. Nigeria, *Lely* 699 (K.), *Lely* ? 10 (K.). Ivory Coast : *Pobeguin* 242 (K.) ; Sierra Leone, *Dawe* 499 (K.). Amboland : Okahanja, *Dinter* 273 (BM.).

The citation of specimens could be almost indefinitely multiplied, for the species occurs throughout Tropical Africa (apart from the high mountains) and reaches the Transvaal. Collectors often speak of it as planted for its medicinal virtues—a single tree in a village. This may partly account for its vast range. The citations illustrate this.

The species is no doubt variable, but I do not think there is more than one concerned. The distinction of the more numerous nerves is, I believe, only a question of age—as the leaf matures they become more noticeable—and the differences in the cutting of the leaf-margins can be seen on the same specimen.

Hiern has some interesting notes on this plant in Welwitsch, Cat. Afr. Plants, loc. cit. p. 428.

2. S. HOCKII, comb. nov. *Peucedanum Hockii* Norman in Contrib. Flor. Katanga, Suppl. ii, p. 98 (1929).

Belgian Congo : Sankisia, *Bequaert* 197 (type Bx.), Elisabethville, *Hock*, s. n. (Bx.). N. Rhodesia : Chikupi, *Sandwith* 120 ; Sheseke Distr., *Miss Gairdner* 226 ; Solwezi Distr., Solwezi, *Milne-Redhead* 1125 (all K.).

Evidently allied to *S. araliacea*, but instead of a tree or bush it is a perennial herb from a woody root-stock. It is entirely leafless at the time of flowering and fruiting, and up to the present leaves are not known. The pedicels are fewer and much more slender than in *S. araliacea*, the fruit almost identical. Hochstetter tells us that the name *Steganotaenia* means ' hidden vitta '. I can only say that in the many mericarps which I have examined from all parts of Tropical Africa in all stages of development I have failed to find true vittae, though I have occasionally found rudimentary ones which are clearly not functional. As a rule, nothing at all is visible. This applies to both species, and was noted in the original description of *S. Hockii*.

Species doubtful and excluded.

Peucedanum altum Hiern, F. T. A. iii, p. 20 = *Peucedanum Petitianum* A. Rich.

P. araliaceum B. & Hk. f., ex Vatke Linnaea, = *Steganotaenia araliacea* Hochst. xl, p. 188 (1876).

P. atropurpureum(Steud. ex A. Rich) Hiern, = *Erythroselinum atropurpureum* (Steud. ex F. T. A. iii, p. 21 A. Rich) Chiovenda.

P. Bequaertii Norman, Plant. Bequaert. iv, = *P. heracleoides* Baker. 2, p. 306.

P. Buchananii Baker, Kew Bull. p. 268 = *Lefebvrea angolensis* Welw. ex Engler. (1897).

P. Dinteri Wolff, Fedde Rep. xvii, p. 153 = *Lefebvrea* (*Upingtoniae* Schinz ?).

P. Elliotii Engler, Pflanzenwelt, Afrikas, iii, = *Afroligusticum chaerophylloides* Norman
   2, p. 825 (1921).   (1927)=*Afroligusticum Elliottii*, comb.
                                    nov.

P. Eminii Engler, Pflanzenwelt Ost-Afrik. = *Pseudocarum Eminii* (Engl.) Wolff.
   C. p. 300.

P. fraxinifolium Hiern, F. T. A. iii, p. 22   = *Steganotaenia araliacea* Hochst.

P. graveolens B. & Hk. f. ex Hiern, F. T. A. = *Anethum graveolens* Linn.
   iii, p. 19.

P. Hockii Norman, Cont. Fl. Katanga, = *Steganotaenia Hockii* Norman.
   Suppl. ii, p. 98.

P. Kingaense Engler, Engler's Jahrb. xxx, = *P. heracleoides* Baker.
   p. 368.

P. Mildbraedii Wolff, Engler's Jahrb. xlviii, = *P. Kerstenii* Engler.
   p. 279.

P. Uhligii Wolff, Engler's Jahrb. xlviii, = *Oenanthe palustris* (Chiov.) Norman.
   p. 281.

P. Ruepollii Engler, Ann. Inst. Bot. Roma, = Genus ?
   vii, p. 23.

Peucedanum Elliotii Engler I have not seen.   Like all the species whose first mention occurs in the ' Pflanzenwelt Afrikas ' it is most inadequately dealt with, and no type-specimen or any other is cited.   However, Dr. Markgraf has kindly informed me that it is founded on *Scott Elliot* 7802 in the Berlin herbarium.   As this is the same number as the type-specimen of *Afroligusticum chaerophylloides* Norman, I presume the new combination given above is required.

I may say that Scott Elliot's specimen under this number at the British Museum makes it quite certain that the plant is not a *Peucedanum*.

Further Notes on the Genera *Fumaria* and *Rupicapnos*.—III.
By H. W. PUGSLEY, B.A., F.L.S.

(PLATE 30)

[Read 15 March 1934]

A SECOND Supplement to the ' Revision of the Genera *Fumaria* and *Rupicapnos* ' was published in the Journal of this Society in 1932, bringing up to date our knowledge of the group in the light of recent discoveries, which had occurred principally in Morocco. During the last two years these plants have continued to be extensively collected in North Africa, and M. A. Faure has succeeded in obtaining two additional species of *Rupicapnos*. In the genus *Fumaria* no new species has actually been discovered, but good material of several plants hitherto imperfectly known has been collected, with the result that *F. mirabilis* Pugsl., described from a solitary fragment gathered near Algiers, is now known both in North Africa and in Spain, and a form characteristic of the cedar-woods near Blida, first seen in 1922 and tentatively placed under *F. flabellata* Gasp., is now recognized as a distinct, if somewhat critical, species. Further, owing to the excellent examples obtained by Messrs. Alston and Sandwith in their Albanian journey of 1933, a fumitory which I described as *F. officinalis* L. var. *ragusina* on the basis of rather poor material found near Ragusa, is now raised to specific rank.

The sequence and method adopted in this paper follow those of the Revision and its two earlier Supplements, and the descriptions of new groups, with italicised chief contrasting characters, have been similarly compiled.

FUMARIA.

SECTIO I. GRANDIFLORA.

As the anomalous species *F. mirabilis* is now transferred to section *Parviflora*, subsection *Latisepalae*, the reference to it in the sectional diagnosis should be expunged.

SUBSECTIO I. **AGRARIAE.**

* Series **Eu-Agrariae.**

1. FUMARIA AGRARIA Lagasca.

Moroccan exsiccatae lately sent out by Frère Sennen as ssp. *major* f. *Beltrani* vel *F. Reuteri* v. *ripariensis* Pau (no. 7761) and as var. *Maximiliani* Maire & Sennen (no. 7762) seem inseparable from typical *F. agraria*. The set

' Jahandiez. no. 212. *F. agraria* v. *major*. Taroudant, 1931,' as represented in Herb. Mus. Brit., is *F. agraria* var. *erostrata* Pugsl.   No examples of *F. major* Badarro have been seen from Morocco.

In the collection of the University of Barcelona there is a specimen of *F. agraria* from the Balearic Islands (Font-Quer, Eivissa, 1918!).

4 *a*. FUMARIA MIRABILIS Pugsley.

This species is now transferred to section *Parviflora*, subsection *Latisepalae*.

*** Series **Anomalae.**

11 *a*. FUMARIA MAIREI Pugsley.   .

When shade-grown the flowers of this species fail not only to develop the normal broad wings of the outer petals, but, like *F. flabellata* Gasp., they produce no purple colouring about the tip of the upper petal.

SUBSECTIO II. **CAPREOLATAE.**

* Series **Eu-Capreolatae.**

12. FUMARIA CAPREOLATA Linn.

While in South Albania in 1933 Messrs. Alston and Sandwith found *F. capreolata* var. *albiflora* Hamm. growing in company with *F. judaica* Boiss. as an apparent native on limestone rocks above Sarandë. This occurrence in the Balkan Peninsula of *F. capreolata*, which is already known from natural stations in Algeria and Morocco, indicates that its range as a truly wild plant is remarkably extensive—perhaps more so than that of any other member of the section *Grandiflora*.

The exsiccata, *F. capreolata* var. *Guruguensis* Sennen, recently distributed by Frère Sennen (no. 7498), appears identical with Hammar's variety *albiflora*.

In his ' Flore du Tibidabo ' (1929) Sennen separates (p. 33) the *F. Queri* of his exsiccata no. 3888 from the original plant on which he founded this name (Sennen no. 1901), renaming the later gathering *F. Planasi*. This plant (no. 3888), together with no. 4175 (*F. Codinae* Sennen), was referred to *F. Bastardii* Bor. in Journ. Linn. Soc., Bot., xlvii, 440 (1927). Material of no. 1901, the original *F. Queri* Sennen & Pau, has lately been examined, and this proves to be a depauperate shade-form of *F. capreolata* var. *speciosa* Hamm. In the ' Flore du Tibidabo ' Sennen briefly describes several new *Fumariae*, three of which have not yet been seen, viz.:—*F. Barnolae*, *F. Bouchonis*, and *F. Leonardi*.

12 *a*. FUMARIA NORMANII, sp. nov.   (Pl. 30, fig. 1.)

Exsicc. Maire, In cedretis Atlantis supra Blida, 1932 (typus in Hb. Pugsley)! C. Norman, Blida, 1922, in Hb. Pugsley!

Fumaria vix robusta, plus minusve ramosa, nonnunquam petiolis cirrhosis scandens.   Folia irregulariter 2–3 pinnatisecta, foliolis in lobos cuneiformes ad oblongos, obtusos mucronatos ad acutos, fissis praedita.   *Racemi* densi,

multi- (10–25-) *flori*, *pedunculis* rectis satis longis *primarii breviores*, reliqui subaequantes vel longiores. *Bracteae* albidæ, oblongo-lanceolatae, acuminatae vel cuspidatae, *pedicellos* fructiferos apice valde incrassatos *arcuato-recurvos fere aequantes*. *Sepala* 5–6 *mm. longa*, 2·5–3 *mm. lata*, ovalia, peltata, *obtusa nervo dorsali excurrente mucronata*, *leviter dentata*, nervo dorsali conspicuo viridiusculo albida. *Corolla speciosa*, 11–13 *mm. longa*, *alba*, verisimiliter haud rubescens; *petalo superiore acuto*, *rostellato*, *alis intense atropurpureis* sursum reflexis apicem haud attingentibus sed carinam paulo superantibus praedito, calcare breviusculo (3–3·5 mm. longo); *petalo inferiore marginibus angustis patulis* apicem haud attingentibus acuto; petalis interioribus apice sursum curvatis atropurpureis. *Fructûs parvi*, 2–2·25 mm. longi, circa 2 mm. lati, *subrotundo-quadrati*, *obtusissimi* vel etiam subretusi, inferne in stipitem pedicelli apice angustiorem breviter contracti, paulo compressi sed obscure carinati, siccitate apicis foveolis distinctis quam in *F. capreolatâ* plane majoribus *laeves*.

F. Normanii, quae cedreta Atlantis supra Blida Algeriae habitat, *F. capreolatae* L. et *F. flabellatae* Gasp. valde affinis est. Per sepala obtusa mucronata, per corollas valde bicolores rostellatasque quamvis latius alatas, et per fructûs foveolas majores a *F. capreolatâ* differt. *F. flabellata* sepalis minoribus acuminatis, corollis latioribus vix rostellatis, fructibusque majoribus rugosis distinguitur. *F. Mairei* Pugsl. propter corollas obtusas late alatas breviter calcaratas facile dignosci potest.

This beautiful Fumitory first came under observation in 1922, when Mr. Cecil Norman, who was then with me in Algeria, collected a single small plant, with good flowers but no fruits, in the cedar-forest near Blida. I was doubtful at the time whether to place it with *F. capreolata* or *F. flabellata*, but eventually mounted the specimen on a sheet of the latter. A year ago Dr. Maire sent for naming more adequate material from the same locality, and then, seeing its small, smooth fruits, I at first referred it to *F. capreolata*. Dr. Maire, however, dissented from this identification and pointed out that the plant appeared to belong to a local race peculiar to the cedar forest of Blida, and comparable in rank with *F. Mairei* of the Kabylie Mountains. The material has therefore been re-examined, together with a further specimen obtained in 1933, and as the floral characters, though resembling those of *F. capreolata* and *F. flabellata*, are distinct from both and yet are not intermediate, and the fruit also is found to exhibit a characteristic feature, the plant is now described as a new species and named after its original discoverer.

In treating the new plant thus it is recognized that its relationship with *F. capreolata*, *F. flabellata*, and *F. Mairei* is very close, and that it is less well marked as a species than most *Fumariae* of this rank. But it certainly does not possess the corolla of *F. capreolata*, which in all its variations never produces wings of the upper petal covering the keel and always shows a well developed spur. It cannot be placed under *F. flabellata*, not only from its smooth fruits, but from its much larger sepals and narrower corolla. And *F. Mairei*,

though with similarly coloured flowers and smooth fruits, is widely different in the truly Agrarian form of its corolla.

13 a. FUMARIA FLABELLATA Gasparrini.

The University of Barcelona possesses specimens of this species from the Balearic Islands (Font-Quer, Mahon, Minorca, 1913!) and also of the hybrid *F. capreolata × flabellata* from the same locality.

* * Series **Macrosepalae.**

15. FUMARIA MACROSEPALA Boissier.

The Barcelona collection includes examples of var. *obscura* Pugsl. collected in the Spanish province of Jaen, and others intermediate between it and the typical species.

SUBSECTIO III. **MURALES.**

* Series **Sub-Agrariae.**

18. FUMARIA BICOLOR Sommier.

Specimens of this plant from the Balearic Islands (Font-Quer, Illa de Colone, &c., Mahon, Minorca, 1913!) have been noted in the Barcelona collection.

* * Series **Eu-Murales.**

20. FUMARIA MUNBYI Boissier & Reuter.   (Pl. 30, fig. 2.)

M. Faure has lately forwarded excellent flowering material of this rare and elegant species, obtained chiefly near Martimprez-du-Kiss, in the Beni-Snassen district of Eastern Morocco, and at Mostaganem, near Oran. The plants collected are all of a robust and rampant habit, with long internodes and relatively sparing foliage. The lower peduncles are uniformly long, often exceeding the racemes when in flower; the upper ones shorter, as would be expected. The racemes, generally many-flowered on the main stems, are dense at first but frequently elongate considerably, and the very long, flexuous pedicels are a conspicuous feature. The whitish sepals are notable in most of the specimens for their deeply laciniate teeth. The corolla scarcely reaches 12 mm. in length and in most examples is distinctly narrow; in colour it is light rose, except in one gathering, where it is nearly white. The extremely small fruits are alike in all the exsiccatae, obtuse rather than subacute, and finely rugulose rather than smooth; in some cases a considerable proportion have been attacked by *Aylax* and are monstrously swollen. M. Faure is to be congratulated on at last obtaining adequate flowering and fruiting specimens of this rare fumitory, from which its characters can be properly judged.

The species with which *F. Munbyi* may be most readily confused is perhaps *F. capreolata*, and particularly the variety *speciosa* Hamm., shade-forms of which sometimes show considerable resemblance. But in *F. capreolata* the bracts are usually larger, the pedicels thicker, the sepals always larger and more entire, and the fruits, if not larger, at least more obtuse,

Of the exsiccatae of this species mentioned in Journ. Linn. Soc., Bot., xlix, p. 101 (1932), M. Faure's examples from Oran and Sidi Chami are no doubt correct, and ' Font-Quer, no. 216,' though rather weak, sufficiently matches them and may be regarded as typical *F. Munbyi*. Dr. Maire's Ketama plant and ' Font-Quer, no. 215 ' differ in their shorter pedicels and larger, apiculate fruits, and are now dealt with under *F. apiculata* Lge.

21. FUMARIA MARTINII Clavaud.

A further Spanish station for this species, noted from Herb. Univ. Barcelona, is Tarragona (Font-Quer, 1915!).

22. FUMARIA SEPIUM Boissier.

The three sets of Moroccan exsiccatae (1930) sent out by Dr. Font-Quer as *F. capreolata*, Mexerah (no. 225), *F. muralis*, El Araix (no. 228), and *F. sepium*, Tetauen (no. 229) are apparently all forms of *F. sepium* Boiss., varying in the size of the flowers. The species sometimes produces extremely fine flowers at the *locus classicus*, Algeciras.

24. FUMARIA APICULATA Lange.

Among the exsiccatae referred to *F. Munbyi* Boiss. & Reut. in Journ. Linn. Soc., Bot., xlix, p. 101 (1932), are two examples which, now that adequate material of this species has been collected, must evidently be placed elsewhere. These are Dr. Maire's specimen, found in 1929 at Ketama, in the Riffian Atlas, and Dr. Font-Quer's set from the same region (Iter Marocc. 1927, no. 215, as *F. Gussonei*). These two examples show short peduncles, and lack both the elongate pedicels characteristic of *F. Munbyi* and its extremely small fruits. In Dr. Maire's plant many of the fruits are unfortunately galled, but such as are not so are obviously larger than in *F. Munbyi* and persistently apiculate. A fumitory apparently identical with this form, obtained at Ketama in 1932 by Sennen and Mauricio, is now in Herb. Mus. Brit., and this has abundance of good fruit quite unlike that of *F. Munbyi*. Dr. Font-Quer's set no. 215, when compared with these two Ketama examples, is evidently identical; and the three plants, from their short peduncles, pedicels of only moderate length, and fair-sized, apiculate fruits, seem to be allied to the Spanish species *F. apiculata* Lge. rather than to *F. Munbyi* Boiss. & Reut. They differ from typical *F. apiculata* by their robuster habit, broader leaf-segments, and more floriferous racemes (especially Dr. Maire's Ketama specimen), by their smaller, more toothed sepals and more broadly winged upper petal, and by their sub-rotund instead of ovate fruits. But they possess the inflorescence and the characteristic smooth apiculate fruit of *F. apiculata*, and it is therefore proposed to refer them to that species as a new variety, thus :—

β. *africana*, var. nov.

Exsicc. Maire, Iter Marocc. xviii, Ketama in Atlante rifano, 1929 (typus)! Font-Quer, Iter Marocc. 1927, no. 215, ut *F. Gussonei*! Sennen & Mauricio, Pl. du Maroc, Ketama, Telata, 1932, ut *F. media* subsp. *muralis*!

2 P 2

Planta interdum robusta petiolis cirrhosis scandens. Foliolorum lobi sæpius late oblongi mucronati. Racemi usque ad 25–flori. Sepala circa 3 mm. longa, 1–1·5 mm. lata, plus minusve irregulariter dentata. Petalum superius alis nonnunquam carinam superantibus præditum. Fructûs 2–2·25 mm. longi ac lati, subrotundi, circa medium latissimi. Aliter ut in typo.

A further new variety from the Riffian Atlas is :—

[Var. *trachycarpa* Emberger & Maire in Bull. Soc. Hist. Nat. Afrique du Nord, xxii, 276 (1931); n. v.

This is characterised by conspicuously rugose fruits and sepals more deeply toothed almost to the apex.]

<div align="center">SECTIO II. PARVIFLORA.</div>

<div align="center">SUBSECTIO IV. LATISEPALAE.</div>

To include the species *F. mirabilis*, transferred from the *Agrariae*, the diagnosis of the subsection should be expanded as shown in italics :—

. . . . . Sepala, *nisi in F. mirabile*, magna . . . . .

29 *a*. FUMARIA MIRABILIS Pugsley.

This plant was first noticed in 1922 in the Herbarium of the University of Algiers, and was described as a new species in 1927 in Journ. Linn. Soc., Bot., xlvii, 432, from a portion of the original specimen, kindly sent by Dr. Maire. It was placed in the subsection *Agrariae* owing to its long narrow sepals and the form of its corolla, but with the proviso that it might prove really to belong to the subsection *Latisepalae*.

During the last two years I have received from M. Faure abundant material, in good condition, of a very distinct fumitory, resembling *F. micrantha* Lag. in habit and foliage, but with flowers which, though small, recall *F. agraria* Lag. M. Faure labelled his first gathering ' *F. agraria* Lag. ? ' These exsiccatae were collected on cultivated ground in the environs of Oran in 1932, and near Martimprez-du-Kiss, in the Beni-Snassen region of Eastern Morocco, in 1932 and 1933. Last winter an identical Spanish specimen from Almacelles, in Western Catalonia, collected by Dr. Font-Quer, was discovered (unnamed) in the collection of Barcelona University. And quite recently another similar gathering (Sennen and Mauricio, Pl. du Maroc, *Fumaria* ——, Muley-Rechid (Illad Settut), champs, 22. 5. 32) has been received in Herb. Mus. Brit. With this material for comparison it is now seen that the solitary specimen gathered by Bucknall in 1906 at Aranjuez, in New Castile, and tentatively referred to *F. agraria* × *micrantha* (Journ. Linn. Soc., Bot., xlix, p. 104), belongs to the same species.

This material, with the exception of Sennen's and Bucknall's, is homogeneous but for the size of its fruits, and is obviously allied to *F. mirabilis*. The description of the species was taken from the only specimen available, consisting of a single small branch, and the habit of the plant was then indeterminable,

The branch, however, with its foliage and racemes, is now found to agree with the recent specimens, which belong to a robust, erect-growing form of cultivated ground. The bracts of the specific type differ from those of M. Faure's and Dr. Font-Quer's plants in being very much longer, and its sepals are longer and remarkably persistent, while in all of M. Faure's exsiccatae they are caducous. The flowers of the original specimen differ but little otherwise from those of the later ones. The few fruits of the type are smaller than in most of the recent specimens and appear submucronulate, but these seem to be the only points of distinction. The Muley-Rechid plant, sent out by Sennen and Mauricio, appears intermediate between the type specimen and Faure's later exsiccatae. Sennen's specimens are complete plants of robust, branched habit, with rather small, late flowers but good fruits. Their bracts do not exceed the pedicels and thus differ from those of the type, but the narrow and remarkably persistent sepals are quite typical. Bucknall's plant seems identical with Sennen's and well shows the long persistent sepals.

Although from the fragmentary nature of the type the plant's characters can only be partially seen, it may reasonably be inferred that in essential features it agrees with the specimens lately collected, and that they must all be held conspecific. But the form discovered by M. Faure certainly differs in its shorter bracts and more particularly in its sepals, and it is therefore treated as a distinct variety and dedicated to its discoverer. As the species was described from fragmentary material the variety is now diagnosed in full :—

β. *Faurei*, var. nov. (Pl. **30**, fig. 3.)

Exsicc. Faure, Martimprez-du-Kiss, Massif des Beni-Snassen, E. Maroc, 25. 5. 32, ut *F. agraria* ? (Typus in Hb. Pugsley)! Idem. 26. 4. 33! Faure, Route de Delmonte, Oran, 1932! Font-Quer, in Catalonia occidentale, Almacelles, 1926, in Hb. Barcin.!

Fumaria robusta, suberecta vel adscendens, satis ramosa, vix scandens. *Folia* plus minusve glauca, foliolis *in lacinias lineari-oblongas* acutas vel leviter mucronatas fissis 3-*pinnatisecta*. *Racemi* floriferi *densi*, fructiferi paulo elongati, *multiflori* (15–25-flori), *subsessiles* vel inferiores breviter pedunculati: pedunculi crassi, angulati. *Bracteae* lineari-oblongae, acuminatae, viridescentes, *pedicellos* fructiferos *erecto-patentes breves* (circa 3 mm. longos) apice valde incrassatos *subaequantes* vel rarius paulo superantes. *Sepala* 2–2·25 *mm. longa*, 1–1·25 *mm. lata, ovata*, saepius inferne subtruncata, vix peltata, acuta, *grosse irregulariter dentata*, plus minusve roseo-tincta, facile caduca. *Corolla circa* 7 *mm. longa*, *pallide rosea*; *petalo superiore alis roseis* sursum reflexis carinam superantibus apicemque attingentibus *obtuso*, calcare rotundato adscendente: *petalo inferiore* (facile libero deflexo) marginibus roseis latiusculis patentibus acutiusculo *subspathulato*: petalis interioribus albidis apice paulo sursum curvatis atro-purpureis. *Fructûs modici ad majusculi*, 2–2·25 mm. longi, 2·2–2·5 mm. lati, *subrotundati*, circa medium latissimi, *obtusissimi* rarius subretusi, parum carinato-compressi, siccitate apicis foveolis obscuris *plane rugosi*.

It will now be seen that while the form and colouring of the flowers of
F. mirabilis recall *F. agraria*, which doubtless led M. Faure at first to suggest
this identification, the fine leaf-cutting and essentially small flowers are charac-
teristic of the section *Parviflora*, and its thick peduncles and pedicels, large
bracts, scarcely spathulate lower petal, and subrotund fruits bring it to the
subsection *Latisepalae*. In this subsection it is most distinct on account
of its relatively small sepals and the colouring of its corolla. Outside the
Latisepalae the only species that might be mistaken for *F. mirabilis* is
F. algeriensis Pugsl., which shows a somewhat similar robust habit and form of
leaf-cutting. But the tiny flowers of *F. algeriensis* are entirely different both
in form and colouring. It is remarkable that this fumitory, one of the most
distinct in the whole genus, should have remained ·so long imperfectly dis-
tinguished.

F. mirabilis is now known not only in its typical form from Maison Carrée,
near Algiers, but as var. *Faurei* at Oran, West Algeria; Martimprez-du-Kiss,
in the Beni-Snassen district of Eastern Morocco; and Almacelles, West Cata-
lonia, in Spain; and as an intermediate form at Muley-Rechid (Illad Settut),
in Morocco; and at Aranjuez, New Castile, in Spain.

31. FUMARIA BRACTEOSA Pomel.

This plant has an interesting distribution, extending eastwards from Morocco
along North Africa to Syria, Mesopotamia, and Western Persia, but apparently
not occurring in Europe.

It seems to have been found in Morocco first by Dr. Braun-Blanquet (as
F. emarginata), and there is now a Moroccan specimen in Herb. Kew (Trethewy,
Marrakech, 1930!). Good examples were obtained in 1933 by M. Faure at
Martimprez-du-Kiss.

SUBSECTIO V. OFFICINALES.

33 *a*. FUMARIA RAGUSINA, sp. nov.   (Pl. 30, fig. 4.)

Fumaria officinalis L. var. '*ragusina* Pugsl. in Journ. Linn. Soc., Bot., xlix,
105 (1932).

Exsicc. Pugsley no. 293! Alston & Sandwith, Fl. S. Albania, 1933, no. 1220!

I collected this plant on the hillside between Ragusa and Gravosa in 1930,
but could find only a few individuals of small size. Their aspect suggested
F. Bastardii×*officinalis*, but, as no other fumitory could be seen in the vicinity,
and they produced good fruit resembling that of *F. officinalis*, I referred the
plant to that species as a new variety.

Last spring (1933) Messrs. Alston and Sandwith, during their expedition in
South Albania, met with this form in better quantity and condition on limestone
rocks by the ruins of the Church of the Forty Saints above Sarandë. The
specimens which they obtained are of rampant growth and with better foliage
than my Ragusan material, and it is now clear that the plant is too distinct
to be retained as a variety of *F. officinalis*. It is therefore proposed to raise
it to specific rank under the varietal name.

F. ragusina, both by its leaf-cutting and the size and form of its corolla, might be placed almost equally well in the section *Grandiflora* or *Parviflora.* Its fruit, however, is scarcely distinguishable from some forms seen in *F. officinalis,* except for its black-spotted apical pits, and hence the plant has been retained in the subsection *Officinales.*

The new species is separable from *F. officinalis* L. in many particulars. Its habit is essentially slenderer and more rampant, with clear green, less dissected foliage. The leaves are only 2–3 pinnatisect, with the segments cut into oblong lobes somewhat as in *F. Bastardii* Bor. The peduncles are slender and not much shorter than the racemes, which are relatively few-(10–20-) flowered. The sepals are broader and more shortly pointed, though equally laciniate. The corolla is larger, reaching 9 mm. in length, and with a more developed and curved spur; the upper petal is less abruptly winged, usually subacute or shortly rostellate; the lower petal is acute or apiculate, and scarcely subspathulate; the two inner petals are rather narrow and apically curved upwards.

Of the other species of the subsection, *F. cilicica* Haussk. differs widely in its robust habit and its stout, extremely floriferous racemes; *F. Boissieri* Haussk. in its very dense racemes and long-apiculate fruits; and *F. micro-stachys* Kralik by its short racemes of smaller flowers and its very large obcordate fruits. *F. rostellata* Knaf, of the subsection *Latisepalae,* which is notable for its rostellate outer petals, produces very much smaller flowers with large sepals and subglobose fruits.

It may be expected, from the occurrence of this plant near Ragusa, and at Sarandë, about 100 miles to the southwards, that it is widely spread over Southern Dalmatia and Albania. It is a little remarkable that it was not previously described from Dalmatia, where the flora has been thoroughly investigated, in marked contrast to Albania, where, until recently, very little botanical exploration has been attempted.

SUBSECTIO VI. **MICROSEPALAE.**

* Series **Ambiguae.**

38. FUMARIA AUSTRALIS Pugsley.

This species has now been found in the Belgian Congo (Scaetta, Ruanda, 1930!).

38 *a.* FUMARIA ALGERIENSIS Pugsley.

This scarce species was collected last year (1933) by Dr. Maire near Tlemcen, and near Ifrane, in the middle Atlas of Morocco. The specimens from the latter station have deeply coloured flowers like those found by M. Faure at Oued-Imbert and Les Trembles, and should perhaps be distinguished as a variety.

** Series **Eu-Microsepalae.**

43. FUMARIA VAILLANTII Loiseleur.

There is a specimen of this species in Herb. Haun. from Lapland, its most northern station known in Europe.

RUPICAPNOS.

SECTIO IV. CALLIANTHOS.

SUBSECTIO I. **PERENNES.**

* Series **Cerefoliae.**

15 *a*. RUPICAPNOS ARGENTEA, sp. nov. (Pl. 30, fig. 5.)

Exsicc. Faure, Tinissane, vers le Ras Foughal, 31.5.32 (typus in Hb. Pugsley)! Eodem loco, 1931! et 1933!

Rupicapnos perennis sed a primo anno florens, glauca, *relative nana, caudice crasso* ramoso decumbente et *caulibus brevissimis* praedita. *Folia parva,* pleraque radicalia, plus minusve carnosa, *intense glauca,* 4–8 cm. longa (petiolo vix crasso incluso), longe petiolata, *oblongo-deltoidea,* foliolis 2–3 paribus breviter petiolatis et segmentis secundariis *in lacinias parvas oblongas acutiusculas* irregulariter fissis 2-3-*pinnatisecta,* primaria simpliciora. *Racemi* corymbiformes, 10–20-*flori,* cum pedunculo vix crassiusculo usque ad 3·5 cm. longo *foliis paulo breviores.* *Bracteae* 1·5–2 mm. longae, *oblongae,* acutae, subintegrae vel obscure serratae; *pedicelli fructiferi graciles,* apice paulo incrassati, *infimi ad 35 mm. longi.* *Sepala* 2·5–3 *mm. longa, circa* 2 *mm. lata, subrotundo-ovata* vel ovata, peltata, subacuta, *basin versus inciso-dentata* vel laciniata, nervo dorsali viridiusculo albida. *Corolla* 12–14 *mm. longa, haud gracilis,* carinis viridibus *albida;* *petalo superiore* marginibus lilacinis apice breviter dilatatis sursum recurvatis *obtuso, calcare* 3–3·5 mm. longo apice rotundato *fere recto;* *petalo inferiore* marginibus lilacinis apice dilatatis *lineari-spathulato obtusiusculo,* basi *gibboso-saccato;* *petalis interioribus* apice sursum curvatis *modice alatis atropurpureis.* Stylus malleiformis. *Fructûs magni,* sine mucrone quadrangulato 2·5–3 mm. longi, 2·5–2·75 mm. lati, *quadrato-subrotundi, obtusissimi, valde mucronati,* inferne parum angustati, satis compressi et plane carinati, in sicco omnino *dense tuberculato-rugosi.*

R. argentea was discovered by M. Faure near Tinissane, in the Beni-Snassen district of Eastern Morocco, in June 1931, as narrated in Journ. Linn. Soc., Bot.,˙ xlix, p. 109 (1932). The specimens then collected were nearly past flowering, and such flowers as were present recalled those of *R. ochracea* Pomel. In May 1932, and again in 1933, M. Faure revisited the station and obtained excellent material with abundance of flowers and fruit.

The new species, by its essentially dwarf habit and finely dissected foliage, resembles *R. ochracea* and *R. platycentra* Pomel. It differs, however, from the

former by its larger and more shortly spurred corolla and its larger and broader fruits; from the latter it may be separated by the reflexed margins and smaller spur of the upper petal and by its squarish instead of ovate-elliptic fruits. In colouring of flower and form of fruit *R. argentea* shows some likeness to *R. cerefolia* Pomel, but this latter is a much larger plant in all its parts. The glaucous hue of the whole plant is much more intense in *R. argentea* than in any of its allies. The new species seems to be best placed in the series *Cerefoliae* between *R. platycentra* and *R. cerefolia*.

** Series Africanae.

17. RUPICAPNOS SPECIOSA Pomel.

Varying forms referable to *R. speciosa* were collected in 1933 by M. Faure in three habitats around Tlemcen, near Oran.

19. RUPICAPNOS AFRICANA (Lamarck) Pugsley.

This species was found in 1933 by Dr. Maire in good condition in a second station (near Maïdnet) in the Cherrat Valley in Western Morocco.

*** Series Pomelianae.

21. RUPICAPNOS POMELIANA Pugsley.

Dr. Maire collected this species in May 1933 near Garrouban (the *locus classicus*), and M. Faure obtained specimens in August at two stations in the same neighbourhood. This material agrees generally with Pomel's original description (as *R. africana*) and with the type-specimen in Herb. Mus. Paris, but the flowers show more dilated outer petals, the lower in the finest corollas being distinctly subspathulate, and a longer spur (about 4 mm.). The very short spur, emphasized in Pomel's account and apparent in the Paris exsiccata, may possibly be due to incomplete development of the flower, but this can hardly be determined without knowledge of the living plant. The form of the spur appears usually to be constant in each species, and was so treated by Pomel. The sepals in the recent specimens are of similar shape, but rather smaller and less toothed than in the type and Pomel's description.

SUBSECTIO II. ANNUAE.

25. RUPICAPNOS ELEGANS, sp. nov. (Pl. 30, fig. 6.)

Exsicc. Faure, Martimprez-du-Kiss, au vallon de Sidi-Azouz. 26.4.33 (typus in Hb. Pugsley!). Eodem loco, 1932! Tinissane, vers le Ras Foughal, 1931!

Planta annua, quam R. gaetula et R. fraterna major, radice longo et caulibus ad 15 cm. longis, interdum ramosis, crassiusculis. *Folia* verisimiliter *paulo carnosa, glauca,* longissime petiolata, usque ad 20 cm. longa (cum petiolo gracili), *anguste oblongo-deltoidea,* foliolis vulgo 2-paribus breviter petiolatis

et segmentis secundariis *in lacinias oblongas mucronatas acutasve* irregulariter· incisis 2-*pinnatisecta*, primaria minus dissecta. *Racemi* corymbiformes, 5–20-*flori*, cum pedunculo (ad 8 cm. longo) *foliis subduplo breviores*. *Bracteae* 1–2 mm. longae, *lanceolatae*, subintegrae, acuminatae; *pedicelli fructiferi filiformes* apice paulo incrassati, *ad* 60 *mm. longi*. *Sepala* 3–3·5 *mm. longa*, 1·5–2 *mm. lata, lanceolata*, vix peltata, saepius longe acuminata, parce sed grosse *laciniato-dentata*, albida. *Corolla* 12–15 *mm. longa, gracilis*, carinis viridibus *albida* vel plus minusve lilacina; *petalo superiore* marginibus apice parum dilatatis patentibus vel deflexis *anguste oblongo subacuto, calcare circa* 4 *mm. longo* curvato; *petalo inferiore* apice marginibus paulo dilatatis *subspathulato, basi gibboso*; *petalis interioribus* apice sursum curvatis *modice alatis atropurpureis*. Stylus ·malleiformis. *Fructûs magni*, sine mucrone longiusculo circa 3 mm. longi, 2·5 mm. lati, *obovati, obtusissimi, mucronati*, inferne in stipitem valde angustati, satis compresso-carinati, siccitate omnino *dense tuberculato-rugosi*.

This elegant plant was collected by M. Faure in May 1932, at Martimprez-du-Kiss, in the Beni-Snassen district of Eastern Morocco, but the specimens then obtained were mostly dwarf examples nearly past flowering. In 1933 he succeeded in finding very much finer material in good flower, and was able to satisfy himself *in situ* that the plant was a true annual. *R. elegans* is clearly separable from the two other annual species of the section; it differs from *R. gaetula* (Maire) Pugsl. in its larger sepals, its much less slender and long-spurred corolla, and its larger fruit; and from *R. fraterna* Pugsl. by its 2-pinnatisect instead of trisect leaves, and its much larger flowers and fruit.

M. Faure's exsiccata from Tinissane, mentioned in Journ. Linn. Soc., Bot., xlix, p. 112, under *R. fraterna*, proves to be weak material of this new species.

EXPLANATION OF PLATE 30.

Fig. 1. Leaflet of *Fumaria Normânii* Pugsl., with flower and fresh and dried fruits.
Fig. 2. Leaflet of *Fumaria Munbyi* Boiss. & Reut., with flower and fresh and dried fruits.
Fig. 3. Leaflet of *Fumaria mirabilis* Pugsl. var. *Faurei* Pugsl., with flower and fresh and dried fruits.
Fig. 4. Leaflet of *Fumaria ragusina* Pugsl., with flower and fresh and dried fruits.
Fig. 5. Leaf of *Rupicapnos argentea* Pugsl., with flower and dried fruit.
Fig. 6. Leaf of *Rupicapnos elegans* Pugsl., with flower and dried fruit.

Foliage all natural size; flowers and fruits, × 2·5.

FUMARIA AND RUPICAPNOS SPP.

INDEX

[A star (*) denotes a name here published for the first time.]

On the life-history of *Gymnogongrus Griffithsiae* Mart. and *Ahnfeltia plicata* Fries.
By BERYL D. GREGORY, M.Sc.   (Communicated by Professor LILY NEWTON, M.Sc., Ph.D., F.L.S.)

(With 26 Figures)

[Read 15 February 1934]

THE classification of the genera *Ahnfeltia* and *Gymnogongrus* has varied with different authors, the incompleteness of our knowledge of their life-histories preventing the use of recognized criteria.   In both genera pustules are present which were originally thought to have been caused by a parasite.

A survey of the literature shows that a number of workers have concerned themselves with the life-histories of these plants.   Schmitz (14) examined *Gymnogongrus Griffithsiae* Mart., which he thought was attacked by *Actinococcus aggregatus* Kütz.   He found what he believed to be evidence of the presence of haustoria.   Gomont (7), working on *Gymnogongrus linearis*, confirmed the view that the nemathecia were external reproductive organs of parasitic organisms.   Both workers also examined *Ahnfeltia*.   They found that the nemathecia of *Sterrocolax* formed what they thought to be rhizoid-like filaments or ' sinkers ', which penetrate obliquely through the cortex of the ' host '.   Brebner (1) grew spores of *Sterrocolax decipiens* in culture and obtained small disc-like structures which he regarded as early stages in the growth of *Ahnfeltia*.   He, therefore, suspected that the so-called *Sterrocolax* was a phase in the life-history of *Ahnfeltia*.   Phillips (10) compiled a table showing that, of eight species of *Gymnogongrus*, including the two British species, only *Gymnogongrus norvegicus* and *G. fastigiatus* were known to have any means of sexual reproduction.   In these two latter species true cystocarps occur.   He records the presence of a parasite bearing tetraspores on all eight species.   In the light of recent work this point is important, because since it is now known that the so-called parasite is the tetrasporic phase of *Gymnogongrus* itself, it is clear, if Phillips's observation is correct, that in this genus the tetrasporic nemathecia must be formed in two ways.   In other words, both the haplo-diplobiontic and the haplobiontic conditions occur in different species.   This will be referred to later in comparison with the genus *Phyllophora*.   Chemin (2) investigated *Gymnogongrus norvegicus* J. Ag. and *G. Griffithsiae* Mart. and their so-called parasites *Actinococcus peltaeformis* Schm. and *A. aggregatus* Kütz.   *Gymnogongrus norvegicus* is one of the species referred to by Phillips in which both tetrasporic nemathecia and cystocarps are known to occur on different plants.   In both Chemin thought he saw evidence of the entry of an external parasite.   Later (3) he carried out some cultural work on *Actinococcus peltaeformis*.   The tetraspores

gave rise to basal discs, which, after two or three months, produced upright shoots closely resembling those of the so-called host, *Gymnogongrus norvegicus*. He concluded, therefore, that *G. norvegicus* is a normal haplo-diplobiontic Floridean, the plant bearing the pustule being, in fact, the asexual tetrasporophyte. His cultural work on the carpospores of *G. norvegicus* (4) confirmed this view. Chemin (5) published a paper on the reproduction of *Ahnfeltia plicata* Fries. He grew the monospores of *Sterrocolax* in culture and obtained from them disc-like structures up to 40 μ in diameter. He concluded that these germlings were probably young *Ahnfeltia* plants. Rosenvinge (12) has since shown that *Sterrocolax* is not a parasite, but an essential part of the *Ahnfeltia* plant, representing its only method of reproduction.

GYMNOGONGRUS GRIFFITHSIAE Mart.

Gymnogongrus Griffithsiae Mart. is an occasional inhabitant of the higher rock pools at Aberystwyth ; individual plants were marked and observed at frequent intervals throughout the year. The plants were examined both in
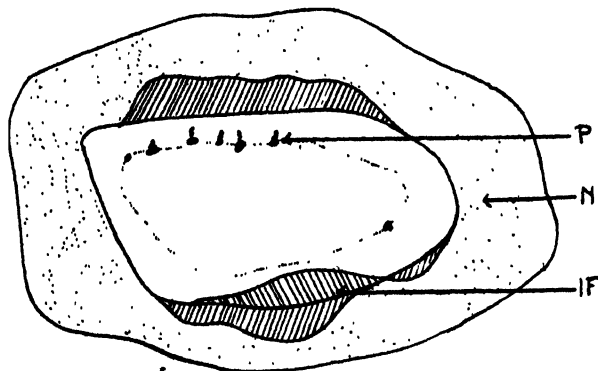
FIG. 1.—T.S. Thallus of *Gymnogongrus Griffithsiae* surrounded by nemathecial tissue (N). Seven procarps (P) occur in the cortical zone. IF, intramatrical filaments. × 80.

the fresh condition and after being fixed in chromacetic acid and sea-water, or in Flemming's weaker solution. Stock material was stored in Calberla's fluid, and it was found, for this plant, that hand sections, mounted in coloured glycerine jelly, were more satisfactory than microtomed preparations.

The plant attains an average height of 2–5 cm., the erect, dichotomously branched, rather mucilaginous shoots arising from a disc-like holdfast. For the greater part of the year even the youngest plants bear lobed, cushion-shaped structures on their thalli, usually near a bifurcation. The confluence of neighbouring pustules is frequent, and in fig. 1 the confluence of pustules has

resulted in a continuous zone of nemathecial tissue surrounding the stipe. Sections through a mature pustule reveal the fact that no sharp line of demarca-
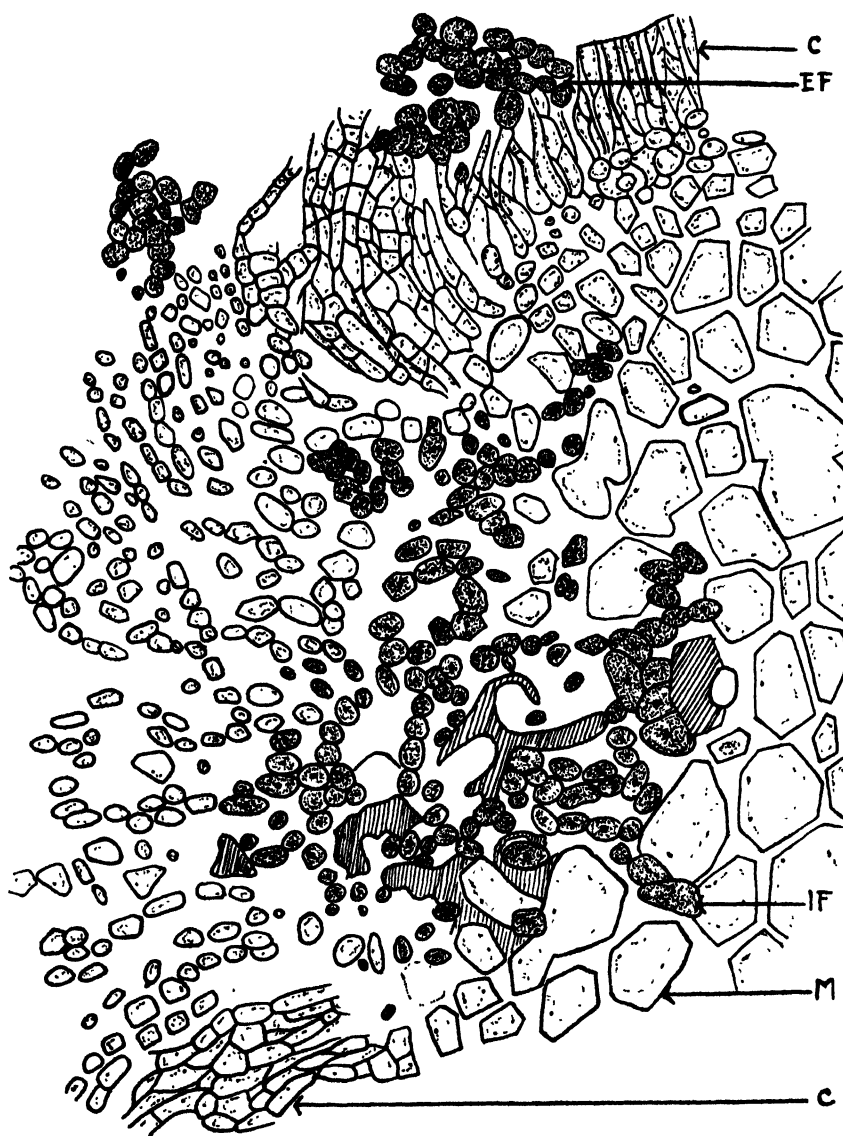
FIG. 2.—T.S. through region of junction between pustule and cortex (C). M, medulla; IF, intramatrical filaments; EF, extramatrical filaments. × 540.

tion exists between the cells of the pustule and the cortical tissue of the thallus (fig. 2). We may for convenience call the region of the pustule within the

cortex the intramatrical tissue, and that outside it the extramatrical zone. The extramatrical tissue can be differentiated into two regions. The part abutting on the cortex consists of several layers of cells which are more or less closely aggregated together and embedded in mucilage. The constituent cells have fairly dense protoplasmic contents, often a very definitely stained nucleus, and several small rhodoplasts. They give rise, towards the exterior, to linear series of cells embedded in mucilage. The cells of this tissue are often clearly uninucleate and possess finely divided rhodoplasts, thus being able to function as photosynthetic organs. The apical cells are usually pointed and abut directly on a very thick ' cuticle ' (fig. 3).
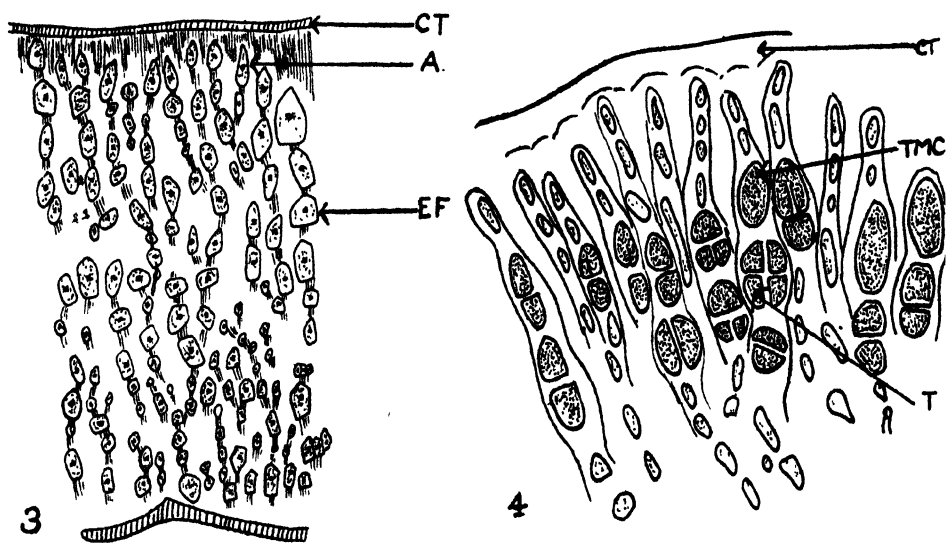
Fig. 3.—A portion of the extramatrical tissue of the pustule, showing the linear series of cells, with their pointed apices (A). CT, cuticle; EF, extramatrical filaments. × 550.

Fig. 4.—A portion of the extramatrical tissue at a later stage, showing the production of tetrasporangia in linear series. T, tetraspore; TMC, tetraspore mother-cell; CT, cuticle. × 560.

During November and December the mucilage of the pustule becomes of a less resistant character. Many of the cells of the extramatrical filaments become converted into tetraspore mother-cells. They assume a rounded or oval shape and four tetraspores are formed, either in a tetrahedral or cruciate manner. The first division takes place at right angles to the longitudinal axis of the filament. The tetrasporangia are formed in a linear series (fig. 4), the apical and basal cells of the filaments remaining sterile. The pointed apical cells have a mechanical function, for, as the filaments are pushed outwards in the ripe pustule, they tend to penetrate and ultimately throw off the thick

' cuticle '.   The spores have an average diameter of 5·4 μ when liberated, and contain dark, reddish-brown contents.   They appear to be slightly amoeboid at the time of liberation.   A second crop of tetraspores may be liberated in the summer months from June to October, and these appear to be the more viable. It was originally thought that only monospores were set free in December, but repeated observation has shown that the actual tetrad division takes place very late, immediately preceding liberation, and also that very large nemathecia may persist for a very long time without the tetrad division taking place. After liberating the spores the pustule decays.

Sexual organs.

No sexual organs have been previously recorded for *Gymnogongrus Griffithsiae* Mart.   The present investigation has shown what appear to be procarps in the neighbourhood of the nemathecium.   These occur at the level of the limiting layer of the cortex.   Their position is shown diagrammatically in fig. 1 and in detail in fig. 5.   Each is composed of an enlarged bearing-cell
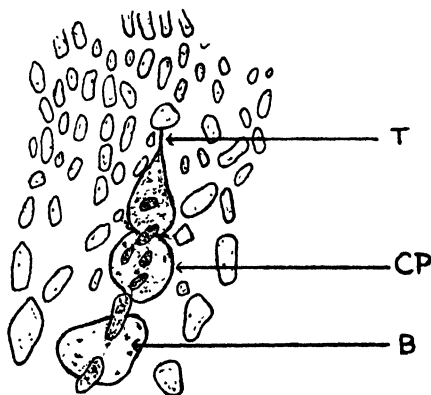
FIG. 5.— A procarp, showing carpogonium (CP) and trichogyne (T).
B, bearing-cell.   × 550.

surmounted by a several-celled carpogonial branch.   Sometimes the bearing-cell is surmounted by one cell with dense protoplasmic contents, a close connection having been established between these and neighbouring cells of the pustule.   In others a two-celled structure is seen above the bearing-cell and in fig. 5 the uppermost of the two cells of the carpogonial branch suggests a carpogonium with its trichogyne.

The presence of spermatia is uncertain, but in one instance a structure (fig. 6) was found in the neighbourhood of a young pustule which suggests

the occurrence of antheridia.   No definite statement, however, can be made, since this is the only record of such a structure.

Development of the pustule.

Examination of material during the months of October and November showed that the bearing-cell of the procarp becomes greatly enlarged, its cell-wall assuming a much thickened and striated appearance (fig. 7).   It has not been ascertained whether this is preceded by a fertilization process.   The bearing-cell then puts out protuberances from which cell-filaments are budded-off. The filaments so formed constitute the intramatrical tissue.   The cells
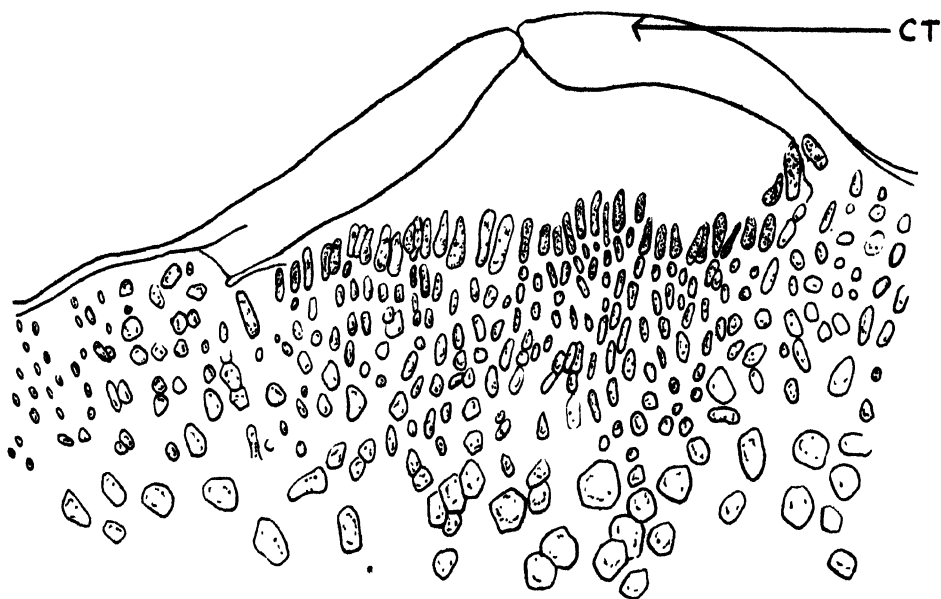
FIG. 6.—A structure which may be the male organ of *Gymnogongrus.*
CT, cuticle.   × 550.

surrounding the bearing-cell and connected with it by plasmodesma in fig. 7 have originated in this way.   An outgrowth is first formed into which proto-plasmic contents pass, and this is finally cut off as a daughter-cell, plasmodesma uniting it with the bearing-cell.   The cells apparently embedded in the bearing- · cell in fig. 8 have been cut off by protuberances arising at right angles to the plane of the section.   In fig. 8 the remains of the carpogonial branch can be seen, the uppermost cell of which was probably a carpogonium.   The filaments (P) lying outside the procarp have originated from the bearing-cell.   They later break through the outer tissues to form the pustule.   The formation of such filaments is clearly seen in fig. 9,
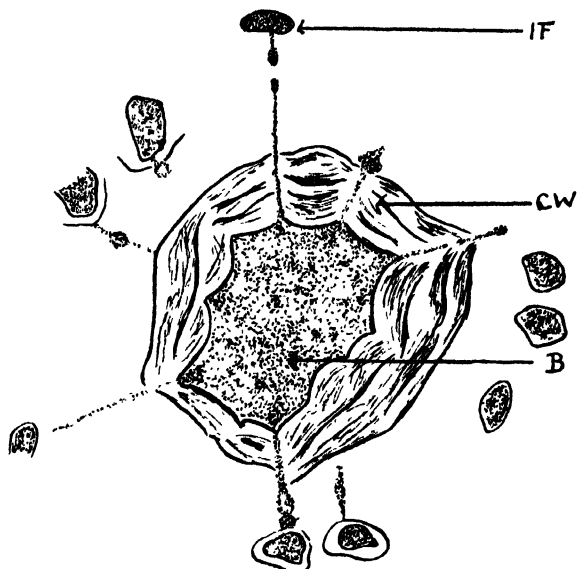
Fig. 7.—The bearing-cell (B) of a procarp, which has become enlarged, with striated, thickened walls (CW). The cells connected with it by plasmodesma constitute the intramatrical filaments (IF). ⅔ 1250.
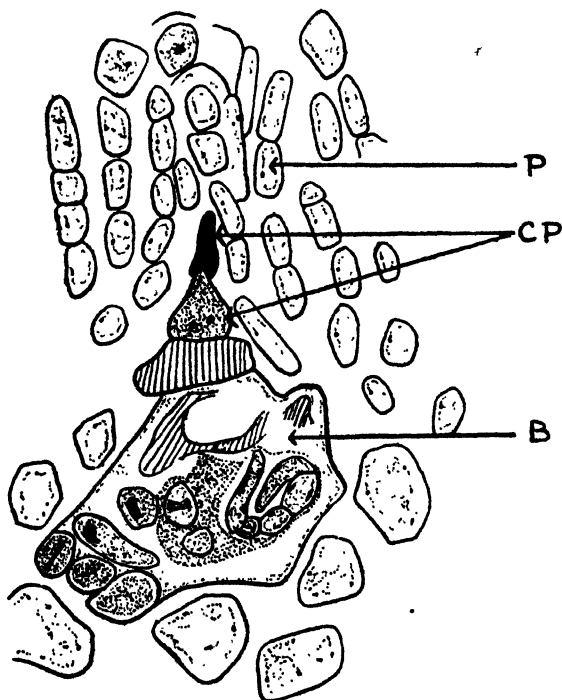
Fig. 8.—Bearing-cell (B) cutting off cell-filaments of intramatrical tissue. The carpogonium is shown; (P) intramatrical filaments cut off by bearing-cell. CP, carpogonial branch, × 1250.

The budding-off of cell-filaments from the bearing-cell results in the production of a more or less fan-shaped mass of tissue directed inwards (figs. 10 & 11). Such tissue presumably has a nutritional function. Ultimately one or more such filaments make their way outwards towards the ' cuticle ' of the host-plant, where they subdivide, pushing the ' cuticle " outwards (fig. 10). This is followed by further subdivision and by the upgrowth of additional intra-matrical filaments until a nemathecial pustule is formed (fig. 11), from which ultimately tetraspores are developed in linear series.
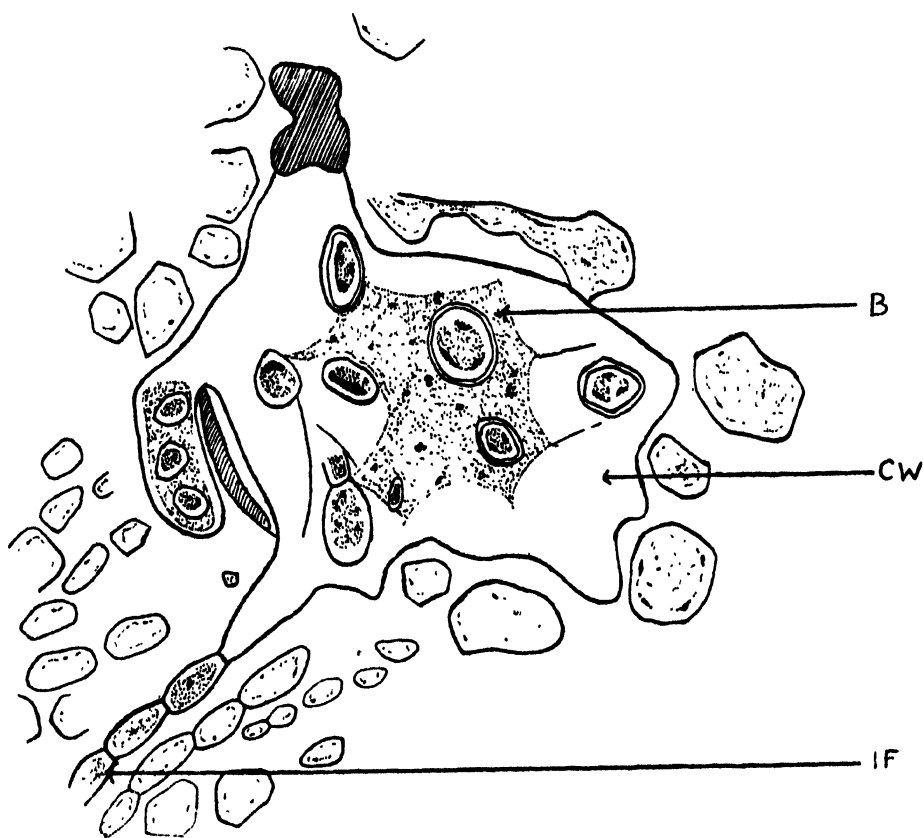
FIG. 9.—Further cutting off of intramatrical filaments (IF) from bearing-cell (B).
CW, striated wall.   × 1250.

It is thus clear that the so-called *Actinococcus* pustule arises as a result of proliferation of the bearing-cell of a *Gymnogongrus* procarp, and it appears that in this latter genus there is the production of a carpo-tetrasporophyte on the sexual plant. A cytological examination of the cells has been made, but as yet the evidence is incomplete.

Spore cultures.

The tetraspores grow extremely slowly in culture, those liberated in December giving rise only to very rudimentary disc-like structures of four to six cells. Those liberated in June showed small discs containing six to sixteen cells, with one or two filaments of several cells projecting from them. Such a condition was evident after about six months, but after a year no further advance was noted. Various sources of nutrient were supplied, but they had little apparent effect upon the rate of growth.
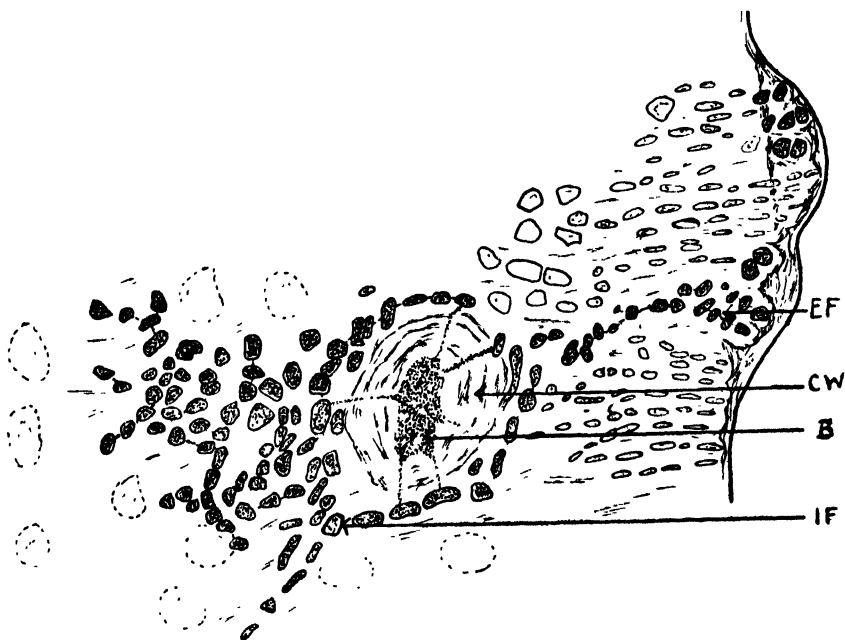
FIG. 10.--The young pustule at a slightly later stage. B, bearing-cell; CW, striated wall; IF, intramatrical filaments; EF, extramatrical filaments forming young pustule. × 550.

AHNFELTIA PLICATA Fries.

Ahnfeltia plicata Fries is a very abundant perennial in the deeper lying rock pools at Aberystwyth. The plants form very sturdy, wiry clumps, frequently attaining a height of 15 cm., consisting of erect shoots with repeated lateral branching, arising from a small disc-like holdfast. From October to March they bear a large number of small encrustations on their thalli, often of a slightly paler colour than the thallus itself. These encrustations have been previously described as the parasitic tubercles of *Sterrocolax decipiens* Schmitz. Individual plants were marked and examined at frequent intervals throughout the year. In this way it was found that some few plants never bore the tubercles. The significance of this will be seen later.
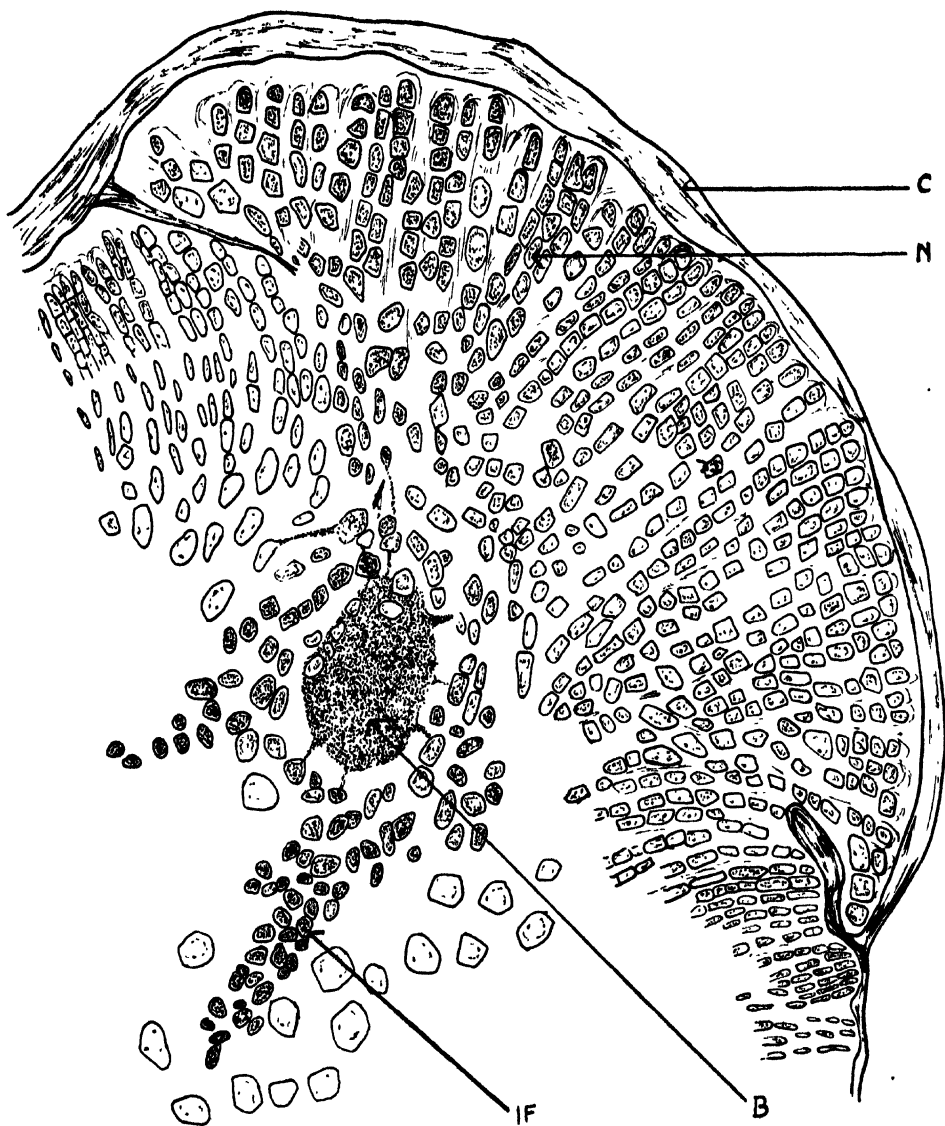
FIG. 11.—T.S. Thallus passing through a young pustule and through the bearing-cell (B)
    from which it arose.   C, cuticle; N, nemathecium; IF, intramatrical filaments.
    × 550.

The thallus of *Ahnfeltia* forms a compact tissue of very small cells. Two regions can be distinguished—an inner medullary region composed of large colourless cells, and an outer cortical or limiting zone composed of more or less cubical cells with small rhodoplasts.

Ahnfeltia plants exposed to rough seas often exhibit a secondary growth in the lower regions of the stipe, such a growth taking the form of concentric zones of secondary tissue formed by the limiting layer.

The pustules consist principally of an extramatrical mass of tissue from which monospores are ultimately liberated. Intramatrical filaments penetrate
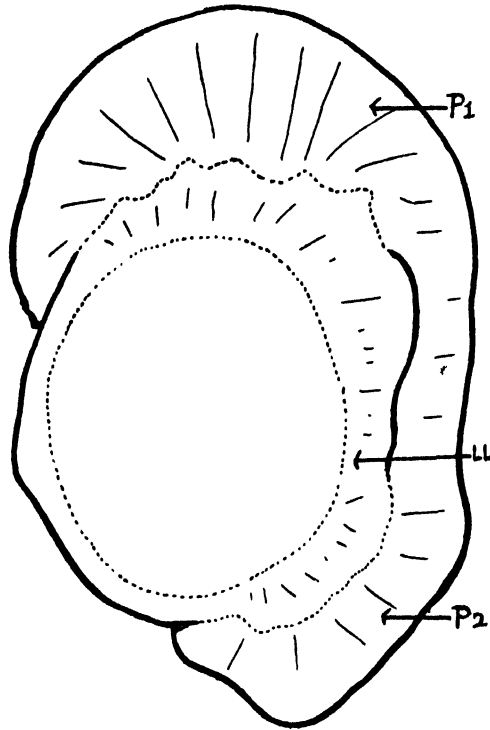
Fig. 12.—Diagram of T.S. Thallus of *Ahnfeltia plicata* showing confluence of two pustules (P₁ P₂). LL, limiting layer. × 120.

between the linear series of cells, constituting the abnormally developed limiting layer of the thallus. The pustules occasionally coalesce (fig. 12). The pustule consists of a mass of small-celled filaments radiating outwards in a very regular manner, delimited on the outside by a very thick 'cuticle'. The cells are uninucleate and contain small rhodoplasts. These septate filaments form a regular pseudo-parenchymatous tissue in the interior of the pustule, but, toward the outer edge, they become separated from one another, and their
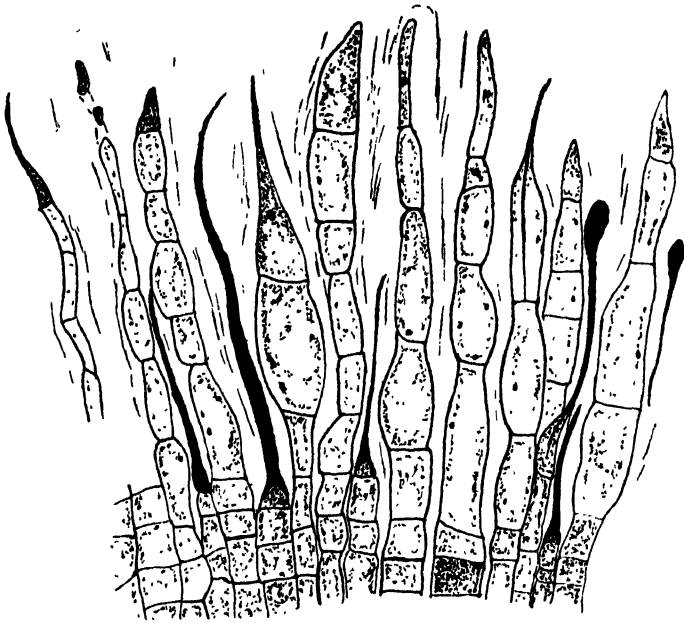
Fig. 13.—Portion of the outer region of an immature monosporic nemathecium.
× 550.
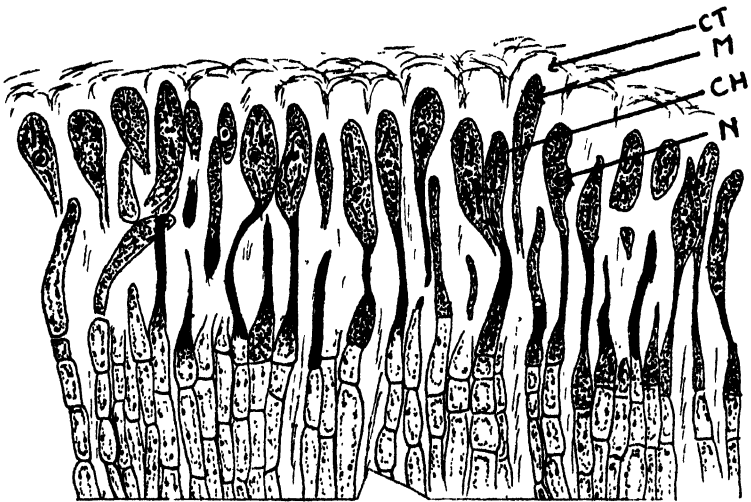
Fig. 14.—As at fig. 13, at a later stage, showing the development of the mono-
sporangia (M).   CT, cuticle; CH, chromatophores; N, nucleus.   × 550.

constituent cells are usually larger. The apices of the filaments are at first long, narrow and pointed and frequently bent (fig. 13). When the pustule has assumed its maximum size, however, the apical cells of the filaments swell out to a club-shaped form (fig. 14), being frequently united to the cell below by a long, thread-like tapering portion. The cells have a nucleus with a very definite nucleolus, and one or two pairs of very characteristic chromatophores. They are often ribbon-like with a curved outline, but other forms occur. They usually lie in parallel pairs. Finally, from these monosporangia, spherical monospores are set free, with an average diameter of 7·2 μ. Schmitz (14) states that, with the formation of monospores, the apical growth of the filament ceases, but that, occasionally, further growth takes place by the activity of neighbouring filaments, which grow past and completely enclose the monospore-bearing series. The appearance of a very large pustule, found in November, favours this view. Normally, at this time of the year, only newly formed pustules are to be found, the previous crop of pustules having disintegrated. In this large pustule four zones of 'secondary growth' were seen, each zone being terminated by a 'monosporic' region. The pustule was probably four years old. The discontinuity, causing the zonal appearance, was formed, presumably, by a pushing aside of the filaments, which bore monospores, through the upgrowth of new filaments.

Development of the pustule.

The first indication of the presence of the pustule is an abnormal development over a restricted area of the limiting layer of the stipe of *Ahnfeltia*. This tissue, which is normally about four cells in width, ultimately forms a wide zone of very regular, more or less cubical, uninucleate cells. The active growth is brought about by the apical division of the cell-filaments (fig. 15). Rosenvinge (12), in a recently published paper on *Ahnfeltia*, calls these newly formed cell-filaments the primary nemathecial filaments. Within such a tissue occur numerous more or less flask-shaped cells which stain very deeply. Their shape is reminiscent of carpogonia. They are the apices of cortical filaments. Such cells frequently arise immediately from cells of the outer medulla, and from the study of serial sections, they appear to move outwards in the developing pustule. They would appear then to push their way between the already existent cell-filaments, thus contributing to the thickness of the cortex. Furthermore, the occurrence of similarly staining cells terminating filaments in the immature pustule itself (fig. 19) would suggest that they also add to the mass of the pustule. Rosenvinge thinks that they may represent sterile hair cells. He considers that they arrest the further growth of the filaments on which they occur, and that they may be reduced organs without function, not giving rise to any new formation. Chemin (5), too, considers them of no significance. In the mature pustule there is no sign of these structures. In fig. 16 is shown the first sign of the nemathecium. It is clear

that it is of internal origin, and is not gaining entrance from without. A slight bulging of the ' cuticle ' is caused by the apical cells of a number of the newly formed cortical filaments having assumed a rounded or club-shaped form.
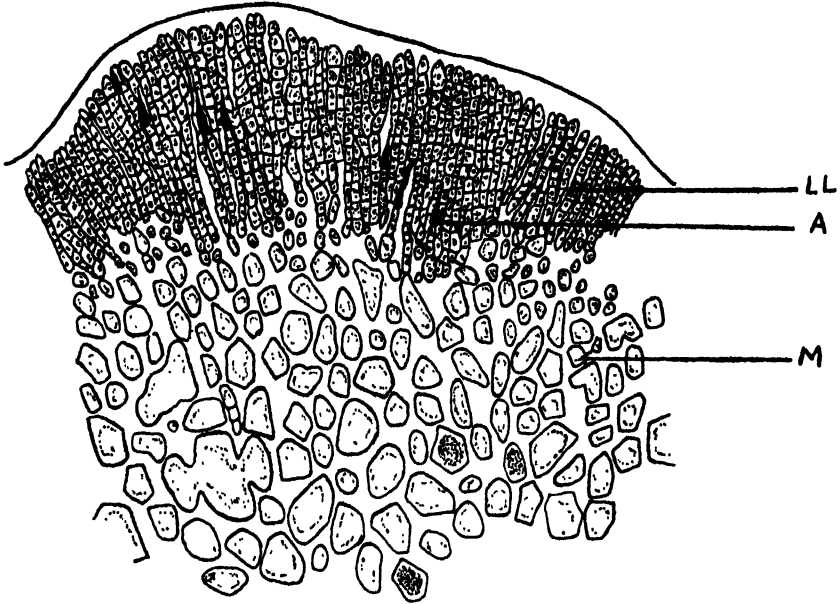
FIG. 15.—T.S. Thallus through abnormally developed cortical region. LL, limiting layer; M, medulla; A, apices of newly developed cortical filaments. × 550.
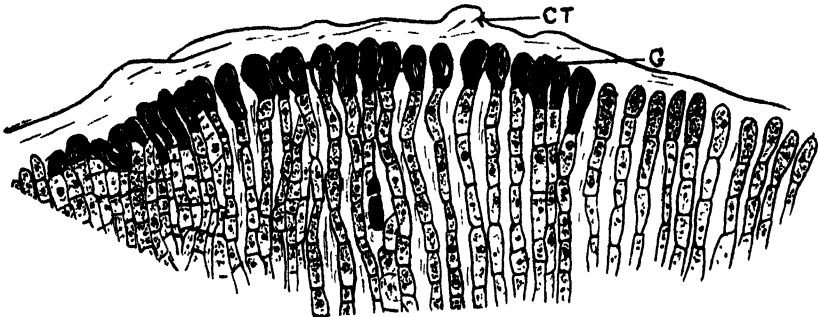
FIG. 16.—T.S. Thallus through abnormally developed cortical region, showing production of ' generative cells' (G). CT, cuticle. × 1250.

These cells stain very deeply. They appear to correspond with Rosenvinge's ' generative cells', which he describes as arising ' at the upper end of the nema-thecial filaments terminally or laterally, singly or usually in small groups,

which seem to arise by division of a single cell '. In the material collected at
Aberystwyth the ' generative ' cells seem always to rise in a terminal position.
In some sections these cells arose in smaller groups, several such groups later
becoming confluent, by the lateral extension of the products of division of these
cells.   At a later stage a number of such groups had coalesced to form a pustule.
Rosenvinge describes generative cells growing out laterally and so giving rise
to a number of different groups of generative cells, but the present investigation
has not confirmed this statement.   The ' generative ' cells give rise to the cell-
filaments of the pustule.   Rosenvinge calls these the secondary nemathecial
filaments.   Their further division to form groups of cells (figs. 17 & 18) and
secondary nemathecial filaments results in the formation of the pustule.   No
actual break in the ' cuticle ' results, because, as the pustule increases in size,
the ' cuticle ' becomes more arched and new material is added to it, thus
enabling it to maintain, and even to increase, its thickness.   It is clear then
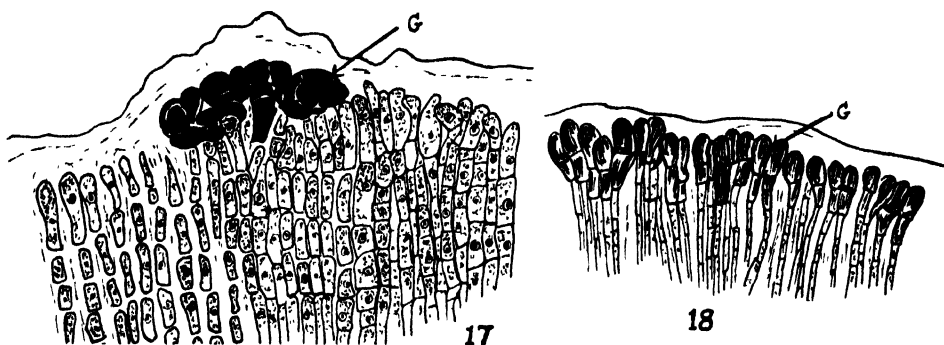
Fig. 17.—T.S.   Very young pustule with cluster of ' generative cells ' (G).   > 1250.
Fic. 18.—T.S.   Pustule at slightly later stage, showing subdivision of ' generative cells ' (G).
      × 1250.

that the pustule originates from certain cells of the hypertrophied cortex.
There is some evidence that, contrary to the views of Rosenvinge and Chemin,
the flask-shaped cells do play some part in the development of the pustule.
They appear to push outwards to the limiting layer and there to form the
generative cells.   Furthermore, when once the generative cells have begun to
form, additional flask-shaped cells may be seen in the pustule.   When the
generative cells are fully developed, at the extremity of the pustule, no further
flask-shaped cells are visible below.

     At the region of union of pustule and thallus tissue there is an apparent
discontinuity (fig. 19).   Chemin (5) states that it is an effect produced by the
bifurcation of the nemathecial filaments at this level.   It would seem, however,
to be due to the more or less irregular subdivision of the generative cells,
resulting in the nemathecial filaments in the pustule not being continuous with
those of the hypertrophied cortex.   Rosenvinge states that the fusions between

cells of different filaments may also contribute to the irregularity. The 'sinkers' described by Schmitz would appear then to be either the groups of generative cells, occurring at the level of the hypertrophied cortex, or the flask-shaped
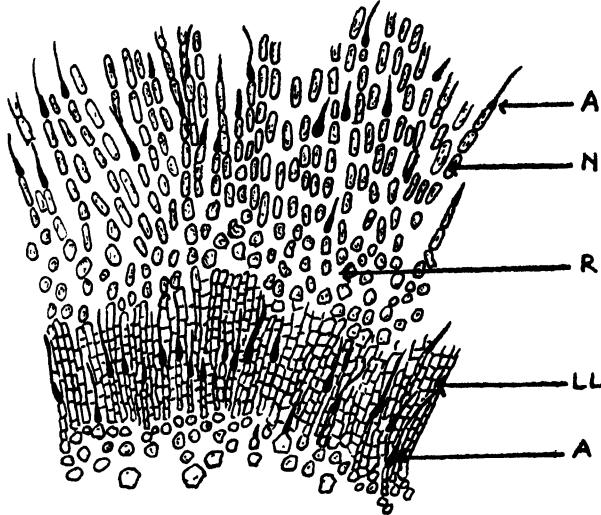
FIG. 19.—T.S. Region of attachment of developing pustule, showing flask-shaped cells (A) in pustule and in cortical zone. R, region of union of nemathecium (N) to limiting layer (LL). × 550.
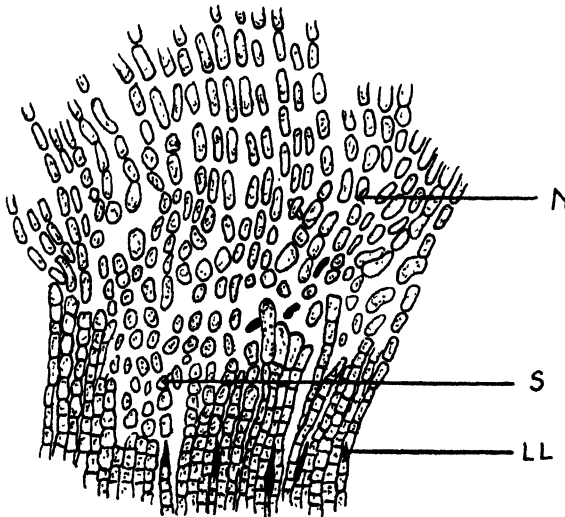
FIG. 20.—T.S. Region of attachment of developing pustule, showing obconical group of 'generative cells' (S). N, nemathecium; LL, limiting layer. × 550.

cells. It is now evident that these are centrifugal in development, and not centripetal as he suggested. A portion of the zone of attachment, showing an obconical group of generative cells, in the hypertrophied cortex, is shown in outline in fig. 20. There is no sign of any sexual apparatus in the young pustule. It is possible that the flask-shaped cells have had some sexual significance in the phylogenetic development of the plant.   In the region of the pustule
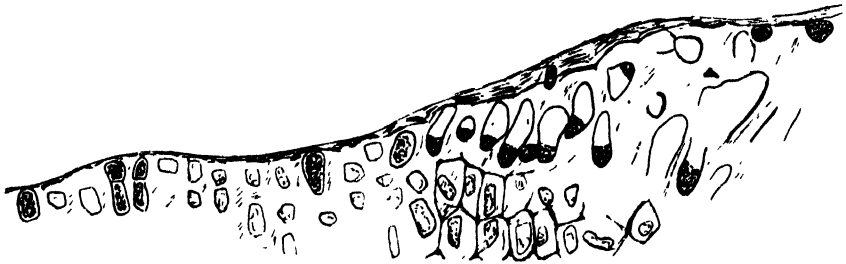
Fig. 21.—T.S.   *Ahnfeltia* passing through spermatangial region.   × 1250.

the medullary cells often undergo peculiar changes, marked, firstly, by dense contents and a large nucleus, and later by the formation of outgrowths between neighbouring cells, resulting in their confluence. It was originally thought that this might represent a reduced form of sexuality, but it appears more likely that it is concerned with the nutrition of the spores. Rosenvinge thinks that the generative cells may be modified female organs.

Male organs.

No male organs have been previously recorded for *Ahnfeltia plicata* Fries. Among the plants examined it was observed, however, that some individuals bore no pustules. They were rather less wiry in texture, and of somewhat
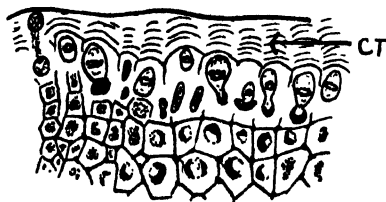
Fig. 22.—T.S.   *Ahnfeltia* passing through spermatangial region.
CT, cuticle.   × 1250.

paler colour, and they have proved to be the male plants. Microtomed series showed that the male organs occur in shallow patches, protected by an extremely thick ' cuticle'.   Fig. 21 shows such a region in which the spermatangia are
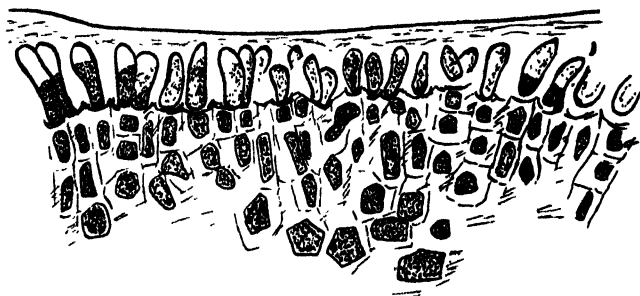
FIG. 23.—T.S.   Spermatangial region of *Ahnfeltia*.   × 1250.
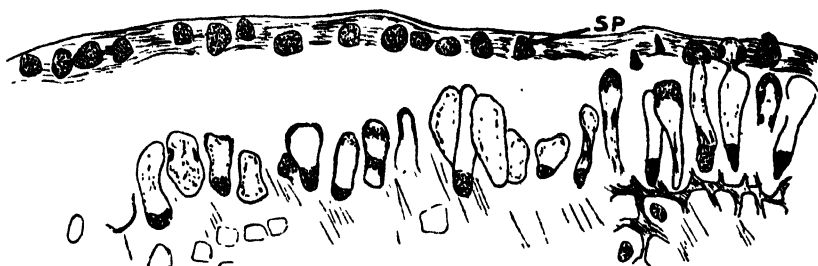
FIG. 24.—T.S.   Thallus, showing development of spermatia (SP).   × 1250.

25

26
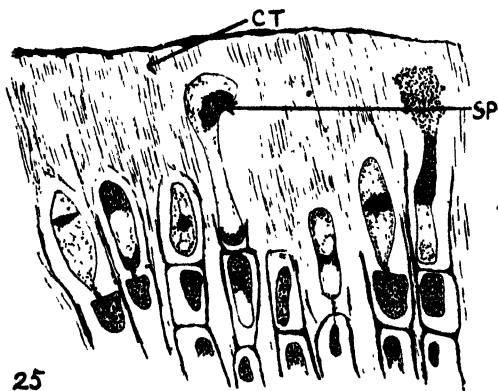
FIG. 25.—T.S.   Thallus, showing striated cuticle (CT) and the formation of spermatia (SP).
          × 1250.
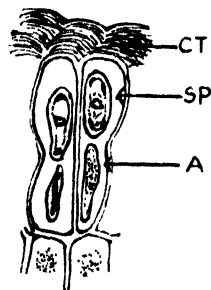
FIG. 26.—Shows production of spermatium in the spermatangium (SP) and sperma-
          tangial mother-cell (A).   CT, cuticle.   × 1300.

seen to be elongated radially, their cell-contents being limited to the base of the spermatangium. Two spermatia are seen embedded in the ' cuticle '. Beyond the main sorus several new spermatangial mother-cells are becoming differentiated. The thick striated ' cuticle ' is shown in fig. 22. Spermatangial mother-cells have cut off spermatangia, which are still of an oval form, with central nucleus. The spermatangia are shown in fig. 23. Fig. 24 shows a number of spermatia embedded in the cuticle, and also spermatia being liberated terminally from two spermatangia. The liberation of a spermatium is shown in greater detail in fig. 25, in which also can be seen the spermatangia and the very thick ' cuticle '. The formation of a spermatangium is seen in fig. 26. The chromatin is arranged in a ring, but it was not possible to make a chromosome count.

DISCUSSION.

This investigation has confirmed the suggestion that the so-called parasites *Actinococcus aggregatus* Kütz. and *Sterrocolax decipiens* Schmitz are in reality a phase of the life-history of their so-called hosts, *Gymnogongrus Griffithsiae* Mart. and *Ahnfeltia plicata* Fries. All the *Gymnogongrus Griffithsiae* plants investigated have been sexual plants, and free-living tetrasporic individuals have not been found. This is of especial interest because two species of this genus, *G. norvegicus* and *G. fastigiatus*, are typical haplo-diplobiontic types, being characterized by tetrasporic and cystocarpic individuals. In *G. Griffithsiae*, however, the carposporophyte phase, as such, is absent. Procarps are present, and possibly, as a result of a fertilization process, the bearing-cell forms ' gonimoblast ' filaments, though the presence of male organs has not been definitely ascertained. However, instead of giving rise to carpospores, they form a massive cortical nemathecium, within which tetraspores are formed in linear series. Rosenvinge (11) and Kylin (9) have shown that a similar condition exists in *Phyllophora Brodiaei*. In this genus there are two types of individuals, the typical haplo-diplobiontic type, represented by *P. membranifolia*, and a second type, represented by *P. Brodiaei*, in which no free-living tetrasporic individuals are recorded. Tetrasporic pustules, which have originated from the bearing-cells of a procarp in a similar manner to those of *Gymnogongrus Griffithsiae*, occur. They were originally described as pustules of *Actinococcus subcutaneus*. In this plant male crypts have also been seen in the neighbourhood of the female organs, the plant being monoecious. If male organs do exist in *Gymnogongrus Griffithsiae*, then this plant would also appear monoecious, since all the plants examined have borne the tetrasporic pustules, and are, therefore, female. Although fertilization has not been observed in *Phyllophora Brodiaei*, Claussen (6) has shown that the nuclei of the gametophytic tissue have four chromosomes, those of the plurinucleate bearing-cell have eight, and he has also shown that reduction-division takes place in the tetraspore mother-cells. It thus appears that in two closely related genera occur species in which a carpo-tetrasporophytic phase has replaced the carposporic and tetrasporic bionts, resulting

in reduction-division occurring at a much earlier stage than in the other haplo-diplobiontic species of these genera.

Liagora tetrasporifera affords another example of a plant with a carpo-tetra-sporophytic phase. Most of the species of this genus have normal cystocarps, whilst tetrasporangia are not known with certainty. In *L. tetrasporifera*, how-ever, filamentous processes are developed in the cystocarps in the normal way, but instead of the end cells forming carpospores they undergo divisions to form a cruciately divided tetrasporangium. This haplobiontic plant, with its diploid gonimoblast filaments, seems to represent an intermediate link between the haplobiontic and the haplo-diplobiontic type of *Phyllophora membranifolia* or *Gymnogongrus norvegicus*, in which reduction-division is delayed until the formation of the tetraspores, in a free-living tetrasporic individual.

The position of the so-called *Sterrocolax decipiens* Schmitz in the life-history of *Ahnfeltia plicata* Fries is somewhat different. The pustule-bearing plants doubtless represent the female sexual individuals, but it appears that true female sexual organs do not exist, although male plants occur, from which spermatia are liberated. The monosporic pustule originates from certain cells of the cortex, after the latter has undergone considerable increase in thick-ness. Rosenvinge has called such cells the generative cells, and thinks they represent a reduced form of sexual organ. The flask-shaped cells, with their peculiar carpogonia-like form, have been described as terminating filaments in the abnormally developed cortex, and it is suggested that these structures may become the generative cells when they reach the outer limit of the cortical filaments. It seemed possible that they might represent vestigial carpogonia, but, as pointed out by Rosenvinge, the terminal position of these structures does not favour this view. He considers, however, that the generative cells, which he maintains have no connexion with the flask-shaped cells, may repre-sent reduced procarps. This is a possible explanation in view of the fact that incompletely developed procarps frequently occur both in *Phyllophora Brodiaei* and *Gymnogongrus Griffithsiae*. The ' secondary' nemathecial filaments, i.e. all the tissue of the visible pustule, would then represent the sporophytic phase. Rosenvinge has shown that both the medullary cells and the monosporangia have four chromosomes in their nuclei. The nature of the pustule is thus difficult to determine, the sexual phase being apparently degenerate, if not entirely lost.

SUMMARY AND CONCLUSIONS.

1. *Actinococcus aggregatus* Kütz. is the asexual biont of *Gymnogongrus Griffithsiae* Mart., developed upon the sexual plant.

2. *Gymnogongrus* bears a large number of procarps, many of which fail to develop further. Others, however, eventually give rise to a pustule. A procarp typically consists of a bearing-cell, surmounted by a two-celled carpogonial branch. Occasionally there are indications of carpogonium and trichogyne. The presence of male organs is uncertain.

3. Ultimately the bearing-cell becomes enlarged and assumes a stellate form, whether as a result of a fertilization process is not known. From it are cut off

a large number of small cells, which remain connected with it by plasmodesma. These cells constitute the intramatrical tissue of the pustule.

4. One or more such filaments grow outwards, collect beneath the ' cuticle ', and eventually give rise to the mature pustule, in which tetraspores are formed in linear series.

5. The so-called *Sterrocolax decipiens* Schmitz is not a parasite, but an integral part of *Ahnfeltia plicata* Fries. It arises as a result of the subdivision of certain cells in the abnormally developed limiting layer, and ultimately, from the apical ends of the nemathecial filaments, monospores are produced.

6. There is no indication of a procarp. It is possible that the origin of the pustule from certain vegetative cells represents a very reduced sexual mode of reproduction.

7. Male *Ahnfeltia* plants occur. The male organs are present in superficial sori, protected by a very thick ' cuticle '. Some of the outermost cells of the cortical filaments function as spermatangial mother-cells. They give rise to elongated, colourless spermatangia, from which spermatia are developed.

8. The presence of spermatia suggests that the pustule is the result of a reduced sexuality, the female organ being now incompletely developed.

This investigation was carried out in the Botany Department of the University College of Wales, Aberystwyth, under the very helpful guidance of Professor Newton.

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On some Marsh Orchids.

By H. W. PUGSLEY, B.A., F.L.S.

(PLATE 31)

[Read 26 April 1934]

INTRODUCTION.

So much has been written on this subject by British botanists in recent years that an apology seems almost necessary for attempting to burden further the already overweighted literature. But the chief result of these writings— the discovery of *Orchis praetermissa* and *O. purpurella* at the expense of losing *O. latifolia*—appears so little satisfactory as to suggest the desirability of further investigations.

In my early days I was susceptible to that weakness for orchids that some never succeed in throwing off. The first Marsh Orchid that I met with was the salmon-coloured *O. incarnata* on the moors of Skye in 1889, and the succeeding summer I found a heavily spotted, rich purple flowered *O. latifolia* at Andermatt in Switzerland. This gave me a very clear idea of the difference between *O. incarnata* and *O. latifolia*. As the latter was represented in our floras as a common British plant, I hunted for it in the following years, always to find what is now known as *O. praetermissa*. For a long period I followed the British *O. latifolia* like a will-o'-the-wisp, worrying my botanical friends for a station for the true plant, which they all seemed to know ; but I never got anything like my Andermatt specimen. Besides *O. praetermissa*, I found nothing better than the dark purple flowered forms of Teesdale and the Scottish Highlands, and occasionally, in the south of England, some showy plants, with spotted leaves and lighter purple flowers, which generally grew in doubtful company. The Report of the Watson Botanical Exchange Club for 1909–10 (pp. 259, 260) contains a note in which I expressed the intention of writing a paper on these plants at some future date, but for the past twenty-four years I have simply collected material during my wanderings, which now amounts to over two hundred gatherings. The discovery of *Orchis cruenta* in the Swiss Alps and a new Marsh Orchis in Ireland during 1933 has at last driven me to action.

The interest lately shown in the British Marsh Orchids seems to have been initiated through a paper by R. B. Ullman and P. M. Hall in Report Winchester College Nat. Hist. Soc. pp. 8–12 (1912–13), which suggested that two plants were passing under the name of *O. incarnata* ; and it was stimulated by the publication of one of these as a new species, *O. praetermissa*, by the late Dr. G. C. Druce (Report B. E. C. iii, 5, 340 (1914)). At that date *O. praetermissa* was

introduced as an addition to the British list, but by 1918 (l.c. v, 1, 162) Druce had become sceptical respecting the existence of *O. latifolia* L. as a definite species.   In 1918 Rolfe (' Orchid Review ', xxvi, 162) reviewed the group, maintaining the Linnean name *O. latifolia* for the plant which Druce had christened *O. praetermissa*.   The following year Col. M. J. Godfery (Journ. Bot. lvii, 137) discussed the probability of the occurrence in Britain of a separate *O. latifolia* L., in which the leaves were spotted.   In 1920 Druce (l.c. v, 5, 576), writing further on *O. praetermissa*, distinguished the dark-flowered form prevalent in Scotland as a new variety, *pulchella* ; and the Messrs. Stephenson came on the scene with an account of a second new British species, *O. purpurella* (Journ. Bot. lviii, 164), and two further papers (l.c. 243 & 257), in which they argued, *inter alia*, that a spotted-leaved *O. latifolia*, distinct from *O. praetermissa*, did exist in Britain.   The last of these papers is illustrated by a useful coloured plate, showing a series of enlarged detached flowers.   Col. Godfery also this year (l.c. 286) wrote maintaining the existence of a British *O. latifolia*. Extended comments on these articles were printed by Druce in Report B. E. C. vi, 3, 309 (1922).   In November 1922, Mr. Wilmott read a paper before the Linnean Society, contending, as Rolfe had done, that *O. latifolia* L. was identical with *O. praetermissa* Druce—a contention in which he was influenced by the fact that specimens recently collected in a Swedish locality, where Linnaeus was known to have seen *O. latifolia*, were identified by Druce with his *O. praetermissa*.   This paper was adversely criticed by Druce (Report B. E. C. vi, 5, 625) and by Col. Godfery (Journ. Bot. lxii, 35 (1924)).   Meanwhile, Messrs. Stephenson had written further on *O. praetermissa* and its variety *pulchella* (Journ. Bot. lxi, 65 (1923)) as well as on *O. incarnata* (l.c. lxi, 273).   After 1924 Messrs. Stephenson turned their attention to the southern Marsh Orchids (l.c. lxiii, 93, and lxvi, 97), and excepting Mr. H. Cary Gilson's ' British Palmate Orchids ' (1930), little more was published in this country until the appearance of Col. Godfery's Monograph of the British Orchidaceae in 1933.   In this work the author retains *O. latifolia* L. (a plant with narrow, spotted leaves), *O. purpurella* Steph., *O. praetermissa* Druce, and *O. incarnata* L. as distinct species.   A similar treatment obtains in Butcher and Strudwick's ' Further Illustrations of British Plants ' (1930).   It will be seen that an element of doubt hangs over the nomenclature of all of these plants owing to the disputed identification in Britain of *O. latifolia* L., the earliest species to be described. Before directly dealing with this point, however, it is desirable to investigate the treatment of the group by pre-Linnean writers.

   In this discussion specific names will be used in the sense in which they are taken in Col. Godfery's Monograph and Butcher and Strudwick's ' Further Illustrations of British Plants ' ; and the broad, spotted leaved Marsh Orchids of the Alps will be mentioned as *O. majalis*,

THE PRE-LINNEAN AUTHORS.

The earliest known reference to a Palmate Orchid occurs in Fuchs's ' Historia' (1542), where (cap. cclxx, 712–713) we find figured *Satyrium basilicum mas* and *Satyrium basilicum femina*, which have been identified without doubt with *Gymnadenia conopsea* and *Orchis maculata*. Fuchs and his successors uniformly placed these plants in one group owing to their palmate tubers. The two plants, with the same figures, re-appear in Dodoens's ' Histoire des Plantes ', p. 158 (1557), but in this author's ' Florum Coronariarum odorata-rumque Historia ' (1568) we read, as translated (p. 216), ' What a recent age has named *Satyrium basilicon* is not of one kind, for there is a greater and a lesser, each with unspotted and spotted leaves.' Dodoens then proceeds to describe the two ' greater ' thus :—1. Majus satyrium basilicon, quod plerique marem appelant, folia habet oblonga, lata et laevia . . . nullis aut omnino vix apparentibus maculis respersa : . . . flores . . . colore dilute pur-pureos, exiguis punctis saturatae purpureae respersos . . . 2. Alterum majus genus, quod feminam vocant, priori tamen minus, folia ejusdem formae promit, sed minora et multis nigris maculis conspersa ; flores . . . colore nunc candidos, alios in purpura vel rubentes, vel dilute ad caeruleum inclinantes, semper magis purpureis punctulis ornatos ac variegatos . . . These two plants are figured as *Satyrium basilicum primum* and *S. b. alterum* in two excellent wood-cuts which were reproduced or imitated in most of the illustrated Herbals up to the end of the seventeenth century. The first figure clearly shows a Marsh Orchid with suberect, unspotted leaves, akin to *O. incarnata* or *O. praeter-missa*. From the broad lip of the flower and Dodoens's remarks on its colouring it may be held to be nearer to the latter. Its habitat is not stated, but is likely to be the Netherlands, where Dodoens was living for many years. The second figure undoubtedly represents the spotted-leaved *O. maculata*. In this work thus originated the view afterwards universally held by the old herbalists of the existence of a ' Male ' Palmate Orchid with unspotted leaves and of a ' Female ' Palmate Orchid whose leaves were spotted.

The next development was due to Lobel, who, according to Pulteney, spent some of his early years in the south of France, and travelled in Switzerland, Italy, Tyrol, and Germany before settling in Belgium and finally in England. It might be expected that, during his travels, Lobel would have noticed various forms of Marsh Orchids, but this is not obvious from his works. In ' Stirpium Historia ', pp. 91 sq. (1576), he distinguishes nine different species, all illustrated by woodcuts. Of these the first two were taken from Dodoens, and the additional seven, like many belonging to other classes of orchids, were adopted from Cornelius Gemma. Of Gemma very little is known, but he was evidently an early enthusiast on orchids. Haller, in his Bibliotheca, mentions that no writings of his are known, but he furnished Lobel with a clavis of the Orchidaceae

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in general, which is printed after the account of the Palmate Orchids in the ' Historia '. Lobel's nine species are :—

1. Palma Christi et Serapias mas folio laevi (Satyrium basilicum primum Dod.)—Floribus dilute purpureis notatis conspersis.
2. Palma Christi Serapias femina (Satyrium basilicum alterum Dod.).
3. Serapias, candido flore, montana, maculatis foliis. C. Gemmae.
4. Serapias palustris latifolia, flore albo subpurpurascente, folio laevi latoque, precocior violaceâ. C. Gemmae.
5. Serapias palustris altera leptophylla, serius florens, coma violacea, foliis interdum laevibus interdum maculosis. C. Gemmae.
6. Serapias montana laevi folio. C. Gemmae.
7. Cynorchis Dracontias, foliis et floribus impense rubris. C. Gemmae. Praecox ; in humidis et uliginosis ubi nigrior terra est.
8. Cynorchis palustris laevi folio leptophyllo omnium vilissima. C. Gemmae.
9. Cynorchis palustris altera lophodes vel nephelodes. C. Gemmae.

The figures of the first two of these plants are those of Dodoens ; the remaining seven original. No. 3 represents a form of *O. maculata* ; no. 4 shows long foliage and bracts, with small, narrow flowers, and is evidently a luxuriant form of *O. incarnata* ; no. 5 has unspotted leaves and suggests *O. praetermissa* ; no. 6 is a doubtful plant with unspotted leaves ; no. 7 has broad spreading foliage, which is said to be deep red like the flowers ; this may possibly be intended for *O. majalis*, wherein the leaves are sometimes so heavily spotted that the whole plant looks purple ; no. 8 seems to be a slender *O. incarnata* ; no. 9 has broad, spreading, and apparently clouded leaves, and very small flowers ; its affinity is uncertain. No descriptions of these plants are given by Lobel, and no habitats are indicated. The figures of this book were afterwards separately issued as a volume of ' Icones ', which was several times reprinted, and they were frequently copied into other later Herbals.

In his last work, the ' Pemptades ' (1583), Dodoens (p. 240) adds a third species from Lobel, *Satyrium basilicum foliosum* (*Serapias palustris latifolia* Lob.) to his former two. He thus admits two kinds of Marsh Orchids with unspotted leaves, and the last being clearly *O. incarnata*, this may indicate that the original *Satyrium basilicum primum* (vel *mas*) was akin to *O. praetermissa*. The relatively broad lip in the figure may, however, be simply due to a draughtsman's inaccuracy.

The ' Kreuterbuch ' of Tabernaemontanus (1588) gives (pp. 1059 sq.) seven of these orchids, the same as Lobel's, excluding nos. 7 & 8, and illustrated by his figures. For six the generic term *Palma Christi* is used. Gerard (Herball, p. 169 (1597)) includes all of Lobel's species, with the names varied and fresh plates more or less similar to the originals. Emanuel Sweert's ' Florilegium ' (1612) has four species only, based on Lobel's ; two, with unspotted leaves, are the same as Dodoens's in the ' Pemptades ' ; two are forms of the spotted-leaved *O. maculata*. The figures are copied from Lobel, but are much cruder. Besler's ' Hortus Eystettensis ' (1613) has four original figures of plants of

this group, which are all doubtfully determinable. No form is portrayed with spotted leaves.

We now come to the ' Pinax ' of Caspar Bauhin (1623), where (p. 85) these plants are placed in a genus *Orchis palmata*. Ten species of Marsh or Spotted Orchids are recognised, nine of which are based on Lobel. The tenth, *O. palmata sambuci odore*, had been distinguished by Clusius (Stirp. Pannon. Hist. 239 (1583)) as *O. Serapias VII*. The first of Bauhin's specific names, *O. palmata pratensis latifolia longis calcaribus*, shows a mixture of synonyms, the first, cited from Hort. Eystt., referring to *Gymnadenia conopsea*, and with this in mind the ' longis calcaribus ' was seemingly added. The other synonyms, however, refer to Lobel's *Serapias mas folio laevi*, and Bauhin's name has been generally understood in this sense by subsequent authors.

Bauhin's ten names are :—

1. O. palmata pratensis latifolia longis calcaribus (Serapias mas folio laevi Lob.).
2. O. palmata pratensis maculata (Serapias femina pratensis Lob.).
3. O. palmata sambuci odore (Orchis Serapias VII Clus.).
4. O. palmata palustris latifolia (Serapias palustris latifolia Lob.).
5. O. palmata palustris altera (Serapias palustris altera leptophylla Lob.).
6. O. palmata palustris tertia (Cynorchis . . . vilissima Lob.).
7. O. palmata palustris maculata (Cynorchis . . . nephelodes Lob.).
8. O. palmata palustris tota rubra (Cynorchis Dracontias Lob.).
9. O. palmata montana altera (Serapias montana laevi folio Lob.).
10. O. palmata montana maculata (Serapias montana candido flore Lob.).

Parkinson (' Theatrum ', p. 1356 (1640)) includes seven of C. Bauhin's species, the excluded being nos. 3, 9, & 10 of the above list. His figures are those of Lobel. In John Bauhin's ' Historia ', pp. 774 sq. (1651), eleven species are admitted under the generic name *Palmata*. Nine of these are founded on Lobel, to which are added *Orchis Serapias VII* of Clusius and a fresh species akin to *O. maculata*. Most of the figures are taken from Lobel, and some partial descriptions are given. No. 1 (*Palma Christi mas laevi folio* Lob.) is stated to grow near Geneva, in meadows by the Arve ; and no. 2 (an *O. maculata* form) in various places near Basle.

The next important work, the ' Historia ' of John Ray (v. ii, p. 1223 (1688)), reduces the number of species to two, *O. palmata pratensis latifolia longis calcaribus* C. B., The Male Handed Orchis or Male Satyrion Royal, and *O. palmata pratensis maculata* C. B., The Female Handed Orchis or Female Satyrion Royal. The first is described as having unspotted leaves, and purple, flesh-coloured, or white flowers. It is said to vary in size and in length of spike, and to flower in May [O. S.]. Ray remarks that it is the plant noticed by Clusius in meadows near London (Stirp. Pannon. Hist. p. 239 (1583)). To these Ray adds, as species insufficiently known, *O. palmata palustris latifolia* C. B., *O. palmata palustris tota rubra* C. B., and *O. palmata palustris maculata* C. B.,

suggesting that the two former do not differ from *O. palmata . . . longis cal-caribus*, and that the third is a marsh form of *O. palmata pratensis maculata*.

In his continuation of Morison's ' Historia Plant. Oxoniensis ' (iii, p. 498 (1699)) the younger Bobart includes six species of the group, using the nomen-clature of C. Bauhin's ' Pinax '. The species are nos. 1, 2, 4, 5, 7, & 8 of the list given above. Of no. 5 (*O. palmata palustris altera*), which had hitherto been credited with violet flowers, Bobart remarks : ' Spica brevis et densiuscula floribus eleganti sanguineo colore decoratis donatur.' The third edition of Ray's ' Synopsis ' (1724) repeats the two species of the ' Historia ', to which Dillenius adds (p. 382) *O. palmata palustris tota rubra*, stated to grow in Cumberland.

Tournefort (Instit. i, p. 434 (1700)) and Boerhave (Plant. Lugd. p. 152 (1720)) both include three species only under C. Bauhin's names, viz. :—*O. palmata . . . longis calcaribus, O. palmata pratensis maculata*, and *O. palmata palustris latifolia*.

Rudbeck (Campi Elysii, pp. 211 sq. (1701)) figures C. Bauhin's ten species and gives one additional—*O. palmata palustris non maculata Lobelii*—to which no synonym is subjoined. The plates, which seem to be original, are crude and differ considerably from Lobel's. That of *O. palmata . . . longis calcaribus* shows suberect but relatively broad leaves, and the only three with spotted foliage (nos. 2, 7, and 10 of the list above) all recall *O. maculata*.

The last pre-Linnean work that invites notice is Vaillant's ' Botanicon Parisiense ' (1727). In this book the author writes, under *O. palmata pratensis latifolia longis calcaribus* C. B. (p. 152) : ' Il fleurit en mai : pour l'ordinaire les petites feuilles qui soutiennent les fleurs, les débordent . . . sa tige est . . . fistuleuse, le vert des feuilles est pâle . . . Il est le plus commun de nos prez.' Of the plant intended detached flowers, showing lined markings on the lip, are figured (pl. 31, ff. 1–5), and these, with the observations, seem to indicate *O. incarnata*. Continuing, Vaillant writes : ' Le 18 juin j'ai trouvé un orchis palmate dans les prairies de Porchefontaine . . . qui a quelque rapport avec le précédent, mais il en diffère (1) il fleurit plus tard (2) les bractées ne débordent pas les fleurs (3) les fleurs sont plus amples (4) sa tige est plus grêle et plus haute (à 20–22 pouces) (5) ses feuilles sont plus longues, pas si larges à la base, d'un vert plus foncé.' The flowers of this, too, are figured (pl. 30, ff. 14 & 15), and show a broader, speckled lip ; and the plant is apparently *O. praetermissa*. Vaillant further describes under a new name a third plant, differing in having spotted leaves, with purple, speckled flowers and fistular stem, which is also common at Porchefontaine and elsewhere. From the synonyms cited this should be a marsh form of *O. maculata*. Its flowers are figured on pl. 31, ff. 9, 10.

It will now be seen that all of these early authors actually knew but two greater Palmate Orchids, viz. :—The Male Satyrion Royal or Marsh Orchid, with unspotted foliage, and the Female Satyrion Royal or Spotted Orchid, with spotted foliage. In all of their works these two species, distinguished by Dodoens in 1568, take a first place. Lobel, it is true, added seven further species adopted from the list of Cornelius Gemma, and these were admitted

by Caspar Bauhin in his ' Pinax ', but little definite information respecting any of them was ever furnished, except the much later observations of the younger Bobart and Dillenius, which are of doubtful value. It is not till we come to Vaillant that more than one Marsh Orchid is really described and located, and it is evident from his remarks that he regarded the plant now known as *O. incarnata* as the common *O. palmata pratensis latifolia longis calcaribus* C. B. or Male Satyrion Royal. It is notable that all the early forms described as having spotted leaves appear to belong to *O. maculata*, and that the widely distributed *O. majalis* of Central Europe was seemingly overlooked. This must probably be attributed to the fact that these writers, with the exception of Lobel, were not extensive travellers, and the majority of them were apparently most familiar with the Netherlands, Northern France, and Southern Britain, where *O. majalis* is absent or uncommon. It is curious, however, that the Bauhins did not distinguish this plant, which is plentiful in Switzerland ; and Clusius, who almost certainly knew it, perhaps presumed that it was included among Lobel's species, and so omitted any reference to it in Stirp. Pannon. Hist., where *O. sambucina* is first described.

The specimens in the Sloane Herbarium throw a little light on this subject. Courten's plants there include an example from Esperou, in the Cevennes (H.S. 56/8), labelled ' *O. palmata angustifolia* ', which resembles *O. Traunsteineri*. Among Petiver's plants is a good specimen (H.S. 40/18) of a tall, large-leaved *O. incarnata*, with a long spike of small flowers and large bracts, which is named in Vaillant's handwriting ' *O. palmata palustris latifolia* C. B. Pin.', indicating that by this name Vaillant understood a luxuriant form of the common Marsh Orchid. Another slender plant, also resembling *O. incarnata*, is H.S. 40/31, labelled by the same hand ' An *Orchis palmata palustris tertia* C. B. Pin. ? ' This species of C. Bauhin was evidently not well known to Vaillant. There is a further specimen, seemingly referable to *O. incarnata*, among Buddle's British plants (H.S. 124/40/17). This is identified with the Male Satyrion Royal under John Bauhin's name, *O. palmata non maculata*. And an excellent example of *O. praetermissa*, of uncertain origin, is H.S. 312/119/1, similarly labelled among Uvedale's exsiccatae.

As the identity of the synonyms' cited by Linnaeus can now be readily established, I will proceed to the consideration of his species and will endeavour to show (1) that *Orchis latifolia* Linn. is the plant generally known in recent years as *O. incarnata* L., (2) that there is no evidence that Linnaeus ever saw a living Marsh Orchid with spotted leaves, and (3) that *O. incarnata* L. was described from a form of *O. sambucina* L.

Orchis latifolia Linn.

Before the taxonomy of the Marsh Orchids can be satisfactorily settled it is necessary first to determine the identity of *O. latifolia* L., which was the earliest species to be described in the binominal system, i.e. in the first edition of ' Species Plantarum ' (1753). As Linnaeus, however, wrote on the Palmate

Orchids in some of his early works, which he cites in ' Species Plantarum ', it may be well to begin by showing how these plants are there treated.

In ' Hortus Cliffortianus ' (1737), under *Orchis* (p. 429), Linnaeus describes three species, a Marsh Orchid, *Gymnadenia conopsea*, and *Orchis pyramidalis*. His account of the first runs :—

' 1. O. radicibus palmatis, bracteis flore longioribus, nectarii labio trifido, cornu germinibus breviore.

O. palmata palustris latifolia.   Bauh. Pin. 86.   Moris. Hist. 3, p. 498, f. 12, t. 15, f. 3.   Boerh. Lugd. 1, p. 152.

Satyrium basilicum foliosum Dod.   Pempt. 241.

Satyrion latifolium.   Swert. Flor. 1, t. 63, f. 7.

Serapias palustris latifolia.   Lob. Hist. 91.

Crescit in pratis humidiusculis Belgii, Sueciae, &c.

Variat foliis maculatis et immaculatis.'

It will be seen that all the synonyms cited refer to one plant, the luxuriant, early-flowering *O. incarnata*, with unspotted leaves, long bracts, and pale flowers, which was originally described by Lobel. With this identification the diagnosis accords, but the notation respecting spotted and unspotted leaves evidently does not agree. The discrepancy may be explained by a reference to Cliffort's Herbarium. The plants of the Hortus Cliffortianus, now in Herb. Mus. Brit., include five sheets (allowing for one mixture) referable to Linnaeus's first species. The first sheet, labelled ' *O. palmata pratensis latifolia longis calcaribus* ', has three good specimens, which can still be seen to be typical *O. incarnata*. A second, not labelled, shows part of a large plant with long leaves and bracts, which apparently is also *O. incarnata*. A third sheet, without label, exhibits typical dwarf *O. incarnata* ; a fourth, also not labelled, has two plants, one good *O. incarnata*, the other *Gymnadenia conopsea*. The last sheet, labelled ' *O. palmata flore carneo* ', has one specimen, which is *O. maculata*. Linnaeus does not mention *O. maculata* in Hort. Cliff., although he must have been aware of the references to it in the earlier Herbals. It is at least as likely to have grown on Cliffort's estate as either of the three species which he describes, and the presence of a specimen in the herbarium apparently indicates that in 1737 Linnaeus did not recognise it as a distinct species, but regarded it as a spotted-leaved form of his no. 1, and so wrote ' Variat foliis maculatis et immaculatis '. With this proviso the Marsh Orchid of Hort. Cliff. is clearly what is now known as *O. incarnata*.

In 1740 Linnaeus produced in Acta Soc. Reg. Scient. Upsaliensis a long paper, ' Species Orchidum ', in which he endeavoured to classify the family and account not only for the plants which he personally knew but for the different names published by his predecessors. The Male and Female Satyrions are here distinguished, and the former appears on p. 15 as *O. bulbis subpalmatis rectis, nectarii cornu conico, labio trilobo integerrimo, bracteis flore longioribus.* This name is supported by a full synonymy, agreeing with that of Hort. Cliff.,

and numerous varieties, taken from the earlier authors, are appended, usually with a consistent set of synonyms where such existed. The varieties are :—

α. O. palmata pratensis latifolia longis calcaribus. Bauh. Pin. 85.

β. O. palmata montana altera. Bauh. Pin. 86.

γ. O. palmata sambuci odore. Bauh. Pin. 86.

δ. O. palmata sambuci odore floribus purpureis. Tourn. Inst. 434.

ε. O. palmata pratensis latifolia longis calcaribus flore carneo. Tourn. Inst. 434.

ζ. O. palmata pratensis latifolia longis calcaribus flore albo. Tourn.

η. O. palmata pratensis latifolia longis calcaribus, cum lituris purpureis. Tourn. Paris, 509.

θ. O. palmata palustris altera. Bauh. Pin. 86.

ι. O. palmata palustris maculata. Bauh. Pin. 86.

The habitat of the species is given as ' In pratis Europae frequens ', but there is no evidence that any of the varieties were actually known to Linnaeus as living plants. It will be noticed that the only form with spotted leaves is the last variety, which is a plant of doubtful affinity ; and that the plant generally intended is *O. incarnata*, as in ' Hortus Cliffortianus '.

Linnaeus made his famous tour in the islands of Gottland and Oeland in the following year (1741), and in the account of his journey, printed in 1745, he mentions (p. 48) that on the 2nd June he found at Rella, in Oeland, three different orchids. These were the species since known as *O. sambucina* (with red, white, or rose-tinted flowers) and *O. maculata*, together with a third kind, *O. palmata palustris non maculata*, which he says was distinct from *O. maculata*. These discoveries are cited in his subsequent works as ' it. oel. 48 '.

The ' Flora Suecica ' was also published in 1745, and in this (p. 261) the Male Satyrion or Marsh Orchid (no. 728) is included with the diagnosis or definition of Act. Upsal. and a reference to ' it. oel. 48 '. The account of the species continues :—

' O. radicibus palmatis, &c. Hort. Cliff. 429.

O. radicibus palmatis, calcare crasso ovario breviori, labello lineis picto. Hall. Helv. 272.

O. palmata pratensis latifolia longis calcaribus. Bauh. Pin. 85. Rudb. Elys. 2, p. 211, f. 1. Vaill. Paris, t. 31, ff. 1–5.

β. O. palmata sambuci odore, floribus exalbidis. Tourn. Inst. 434.

O. palmata sambuci odore. Bauh. Pin. 86. Rudb. Elys. 2, p. 213, f. 9. Satyrium flore luteo. Rupp. Jen. 284.

Hab. in pratis montosis siccioribus, minus frequens in plerisque regionibus : Stockholmiae in Mariaeberg et alibi '.

The notable features of this description are (1) the change in the synonymy from C. Bauhin's *O. palmata palustris latifolia* to his better known *O. palmata pratensis latifolia longis calcaribus*, which in Act. Upsal. Linnaeus had cited

for var. α ; (2) the additional citation from Haller's ' Enumeratio Stirpium
Helvetiae ', i, p. 272 (1742), where all known forms of the group are included ;
and (3) the retention of a single variety only, *O. palmata sambuci odore*. It
will be noted that ' it. oel. 48 ' is quoted under the species, but not under the
variety.

We now reach the ' Species Plantarum ' (1753), which fixes the application
of the name *O. latifolia* L.   Under *Orchis* (p. 941) the account runs thus :—

' 11. *O. latifolia*—O. bulbis subpalmatis rectis, nectarii cornu conico, labio
    trilobo lateribus reflexo, bracteis flore longioribus.   Act. Ups. 1740,
    p. 15.   Fl. Suec. 728.   It. Oel. 48.   Dalib. Paris, 274.

    O. radicibus palmatis, bracteis flore longioribus, nectarii labio trifido,
    cornu germinibus breviore.   Hort. Cliff. 429.

    O. palmata pratensis latifolia longis calcaribus.   Bauh. Pin. 85.   Vaill.
    Paris, t. 31, ff. 1–5.

    β. O. palmata palustris latifolia.   Bauh. Pin. 86.

    γ. O. palmata montana altera.   Bauh. Pin. 86.

    δ. O. palmata sambuci odore.   Bauh. Pin. 86.

    ε. O. palmata palustris maculata.   Bauh. Pin. 86.

    Hab. in Europae pratis.   ♃ .

    Petala 2 lateralia sursum flexa ;   tres vero conniventia.   Nectarii
    labium lateribus reflexum '.

This is followed (p. 942) by 12. *O. maculata*, which is defined as ' O. bulbis
palmatis patentibus, nectarii cornu germinibus breviore ; labio plano, petalis
dorsalibus erectis '.

The feature that arrests attention here is the addition to the definition of
O. latifolia of ' labio . . . lateribus reflexo ', which is repeated in the description
and contrasts with the ' labio plano ' of *O. maculata*.   The laterally reflexed
lip is a salient feature of *O. incarnata*, when fresh, and its introduction into
Linnaeus's account shows that he was acquainted with the living plant and was
describing an *incarnata*-like form.   The citation ' it. oel. 48 ' shows further that
Linnaeus considered the *O. palmata palustris non maculata*, which he saw at
Rella, to be the same species—an identification the correctness of which was con-
firmed by Fries, who collected the plant (vide Hb. Norm. vii, 65, as *O. incarnata*)
at this station, and more recently by Mr. Wilmott, who obtained specimens
from Rella through Mr. Edwards, of the National History Museum, which
likewise proved to be *O. incarnata*.   These specimens, when first dried, still
showed the characteristic lined marking of the lip (Journ. Bot. lxii, 36).   The
three other synonyms that Linnaeus quotes from his previous works have
already been shown to be *O. incarnata*, and the fresh citation from Dalibard's
' Florae Parisiensis Prodromus ' (1749) adds no new element to the synonymy,
for Dalibard's plant is based on these earlier descriptions of Linnaeus.   The
last synonym quoted, '*O. palmata pratensis latifolia longis calcaribus*. Bauh. Pin.
85, Vaill. Paris, t. 31, ff. 1–5 ', indicates that Linneaus had in view the plant

which Vaillant had described and figured under this name, and this again was *O. incarnata*.

It thus appears (1) that Linnaeus's specific diagnosis or definition and his description of typical *O. latifolia* refer to the plant that in recent times has been regarded as *O. incarnata* L.; (2) that his synonyms all relate to a similar plant; and (3) that his note in Hort. Cliff. respecting spotted and unspotted leaves is due to the fact that in 1737 he did not distinguish *O. maculata* as a different species.

Of living Marsh Orchids known to Linnaeus, that which grew at Hartecamp, and which he described in Hort. Cliff., has been demonstrated to be *O. incarnata*, as was also that which he saw at Rella, in Oeland, which, incidentally, is the common Marsh Orchid of Sweden. And, in a letter to Haller, written from Paris and dated 22/6/1738, Linnaeus says that during a month's visit he had seen nearly all Vaillant's orchids, which presumably implies the inclusion of the *O. incarnata* of which he cites Vaillant's figure. These are the only living examples with which he was acquainted, so far as can be traced, excepting the specimen of *O. latifolia* in the Linnean Herbarium, named by Linnaeus, which, though less characteristic than the examples in Hort. Cliff., is no doubt the same *O. incarnata*. It is the upper portion of a large plant of unknown origin, gathered rather late and with leaves somewhat broader than usual. Its foliage is affected with rust-marks such as are frequently seen on the leaves of orchids, which it has been foolishly suggested are the remains of leaf-spots. The foliage of the specimen shows nothing to indicate whether it was spotted or not, but it was presumably unspotted. According to Dr. Jackson's list it was placed in the Herbarium before 1753, and it may therefore be regarded as the specific type. But its condition is too poor for the accurate determination of its features. It is thus evident that Linnaeus's description of *O. latifolia*, his synonyms, his herbarium specimen, and all the remaining authentic examples that have been traced, alike belong to *O. incarnata*, which should consequently revert to its earlier, validly published Linnean name, *Orchis latifolia*.

Of Linnaeus's four varieties of *O. latifolia*, the first and best known, *O. palmata palustris latifolia*, is obviously a luxuriant form of *O. incarnata*. The third, *O. palmata sambuci odore*, is a distinct plant, subsequently separated by Linnaeus as a new species, *O. sambucina*. The remaining two, *O. palmata montana altera* and *O. palmata palustris maculata*, are founded on two of Lobel's species adopted from C. Gemma, and never really known to any later author or to Linnaeus.

The apparent unsuitability of the specific epithet ' latifolia ', when properly applied to the plant known as *O. incarnata*, will perhaps occur to many botanists. It was evidently taken by Linnaeus from a character attributed to several forms of this group by the early authors, not in comparison with the foliage of another Marsh Orchid or of *O. maculata*, but as contrasted with the relatively narrow leaves of *Gymnadenia conopsea* and *G. odoratissima*, which were then included among the *Orchides Palmatae*.

ORCHIS INCARNATA LINN.

It was the custom of Linnaeus to keep interleaved copies of his taxonomic works in which he inserted additions and emendations for future use, and his volumes are now preserved in the Library of the Linnean Society. The annotated copy of the ' Flora Suecica ' (1745) contains against no. 728 (*O. latifolia*) a somewhat lengthy note in Linnaeus's handwriting, in which an *O. incarnata* is described and distinguished -from *O. latifolia*. As *O. incarnata* was not embodied in Sp. Plant. (1753) the note was presumably written after that date. In the similarly interleaved copy of ' Species Plantarum ' the variety δ of *O. latifolia* (*O. palmata sambuci odore*) is struck out and a MS. note inserted by Linnaeus raising it to specific rank as *O. sambucina*, which is described and contrasted with *O. latifolia* ; this note makes no allusion to *O. incarnata*.

The two new species, *O. incarnata* and *O. sambucina*, were printed in the second edition of ' Flora Suecica ' (1755), where (p. 312) they follow *O. latifolia* (no. 801). In this edition the account of *O. latifolia* is repeated from that in Sp. Plant., with the omission of the synonym from Dalibard and the addition of a figure from Rudbeck's ' Campi Elysii ' (ii. p. 211, f. 1), which agrees with the synonym cited from C. Bauhin. The varieties are excluded, as in Fl. Suec., ed. 1, and an observation is added, based on the MS. note in the first edition, which reads ' . . . . Folia parum maculata, praesertim inferiora, Petala 2 dorsalia patentia . . . Nectarii labium retrorsum complicatum, serratum, obscure trilobum. Floret cum Paeonia flore simplici '. This is followed by the two additional species :—

' 802. *O. incarnata*. Bulbis palmatis, nectarii cornu conico ; labio obscure trilobo serrato, petalis dorsalibus reflexis.

    O. palmata lutea, floris labio maculato. Segr. Veron. 3, p. 249, t. 8, f. 5.

    Hab. in pratis rarius. .

Obs. Praecedenti simillima a qua differt : Foliis pallide virentibus immaculatis, nec saturate viridibus maculatis. Caule dimidio breviore. Bracteis vix flore aut germine longioribus. Corollis pallide incarnatis nec rubris. Petalis 2 dorsalibus totaliter reflexis, nec tantum patulis, nec maculatis ; nectarii labium structura convenit.

803. *O. sambucina*. Bulbis subpalmatis rectis, nectarii cornu conico, labio ovato subtrilobo, bracteis longitudine florum.

    O. palmata, sambuci odore, floribus albidis. Tourn. Inst. 435. . . . .

    O. palmata sambuci odore. Bauh. Pin. 86. Rudb. Elys. ii, p. 213, f. 9. O. foetida sylvatica praecox . . . Hall. Rupp. 297. O. pannonica VIII. Clus. Hist. ii, p. 269.

    β. O. palmata sambuci odore, floribus purpureis. Tourn. Inst. 435.

    Hab. Holmiae, &c.'

A full description follows, ending ' Distinguitur facile ab *O. latifolia* floribus paucis, caule infra medium tantum folioso, bracteis floribus minime longioribus, foliis nequaquam ex ovato-lanceolatis sed lingulatis ut in *O. macula* [sic].'

The account of *O. incarnata*, excepting its synonym, is taken from the MS. note in the first edition ; that of *O. sambucina* follows largely the MS. note in Sp. Plant.

The arrangement of these plants, as here treated by Linnaeus, is not easy to understand. *O. latifolia* had already been described and validly published, and was a generally well-known species. *O. sambucina*, hitherto regarded as a variety of *O. latifolia* by Linnaeus, was an unmistakable plant that had also been known since the time of Clusius. The difficulty arises over *O. incarnata*. Linnaeus's definition of this species contains only one salient feature, the serrate lip, and the sole synonym on which it is based is a North Italian plant afterwards shown to be *O. sambucina*. In his ' observation ' Linnaeus says that it is very like the preceding (*O. latifolia*), but differs by pale green, unspotted, instead of deep green, spotted foliage ; by its stem being only half as high ; its bracts scarcely exceeding the flowers ; the corolla pale flesh-coloured and not red ; and its dorsal petals completely reflexed and not spotted. Recent botanists have assumed that Linnaeus was here describing the plant which they regard as *O. incarnata*, but the actual wording rather indicates a pink-flowered *O. sambucina*, with which all the characters agree. On the other hand, the dwarf stature, short bracts, and unspotted petals certainly do not square with *O. incarnata* ; and under this interpretation the description accords with the synonym cited. Linnaeus had been long familiar with ' *O. incarnata* ', which he had described as *O. latifolia*, and if he had wished to re-name this plant *O. incarnata* and apply the name *O. latifolia* to a different plant with spotted leaves, he would have transferred the description in Sp. Plant., with its synonyms *en bloc*, to *O. incarnata*, and would have rewritten the account of *O. latifolia*. The truth seems to be that Linnaeus, sometime between 1753 and 1755, met with a flesh-coloured *O. sambucina* that he did not understand, and wrote the MS. note in his ' Flora Suecica ', distinguishing it from his *O. latifolia*, to which he inexplicably attributed the character of spotted foliage. At some other date between the same two years, he came to the conclusion that his *O. latifolia* var. δ should be raised to specific rank, and so inserted a description of it as *O. sambucina* in his working copy of Sp. Plant. without reference to his note in Fl. Suecica. In bringing out the second edition of ' Flora Suecica ' he incorporated the two species from the different sources, apparently without realising that they were forms of the same plant. It may be objected to this that there is an authentic specimen of *O. incarnata* in the Linnean Herbarium which is not *O. sambucina*. The Herbarium does contain a sheet named ' *incarnata* ' by Linnaeus, and the specimen belongs to what is now understood under that name. But, according to Jackson's Index, the specimen was not in the Herbarium in 1755, when the species was published, and Linnaeus's MS. list of that year does not contain the names *O. incarnata* and *O. sambucina*.

The specimen, therefore, cannot be held to be a nomenclatural type, and as a type it would agree neither with the description nor the synonym on which the species is based. The name essentially depends on the description, and as this, like the synonym, seems to refer to a form of *O. sambucina*, the name ' *O. incarnata* L. Fl. Suec. ed. 2, p. 312, non ejusdem herb.' can only be regarded as a synonym or variety of *O. sambucina*, which was more clearly described and published by Linnaeus simultaneously with it. If it could be shown that the account of *O. incarnata* referred to *O. latifolia*, the former name would still be a synonym only, owing to the priority of the latter.

The new species *O. incarnata* L. was soon criticised by Haller, who (Emend. in Act. Helvet. iv, p. 151 (1760)) pointed out the identity of *O. palmata lutea* Seguier and *O. palmata sambuci odore* C. B., on which Linnaeus's two species *O. incarnata* and *O. sambucina* were founded.

In the second edition of Sp. Plant. (1763) Linnaeus proceeded to correct the blunder that he had made over *O. incarnata* and the spotted-leaved *O. latifolia* in ' Flora Suecica ', ed. 2.

The account of *O. latifolia* given in Sp. Plant. ed. 1, is retained (p. 1334) with the exclusion of var. δ, and ' caulis fistulosus ' is added to the description. The ' observation ' added in Fl. Suecica, ed. 2, with the reference to spotted leaves, is wholly deleted.

The next species is now not *O. incarnata* but *O. sambucina*, which is not materially altered.

After *O. sambucina* appears (p. 1335) *O. incarnata*, as follows :—

' Bulbis palmatis, nectarii cornu conico ; labio obsolete trilobo serrato ; petalis dorsalibus reflexis. Fl. Suec. 2, no. 802.
O. palmata lutea, floris labio maculato. Segr. Veron. p. 249, t. 8, f. 5.
Hab. in Europa.'

The ' observation ' in Fl. Suecica, ed. 2, with the description distinguishing the plant from *O. latifolia*, has been struck out.

In 1768 the second volume of Haller's ' Historia Stirpium Helvetiae ' was published, which (p. 142) gives a full description and a good figure (no. 1279, t. 32) of the Swiss *O. majalis*, under the name of *O. radicibus palmatis, caule fistuloso, bracteis maximis, labello trifido serrato, medio segmento obtuso.* Haller states that he refers to this species innumerable plants of the fathers, and cites as synonyms the first eight of C. Bauhin's species in the ' Pinax ' with the exception of *O. palmata sambuci odore*. From his treatment of the group Haller seems to have known well the Swiss Marsh Orchids, but not the forms· of north-west Europe which he united with it. Haller's next species (no. 1280) is *O. radicibus palmatis, bracteis coloratis, labello circumserrato trilobato, lobo medio emarginato*, which includes both *O. sambucina* and *O. incarnata*. Haller here again criticises Linnaeus's separation of these plants as two species.

Linnaeus's interleaved copy of Sp. Plant. ed. 2, contains some interesting MS. notes evidently made after a perusal of this work of Haller's. Against *O. latifolia* he copied the definition of Haller no. 1279, and added ' Simile *O. maculatae*

sed folia non maculata et bracteae flore longiores '. ' Oeder 266 ' is also inserted, a reference to Flora Danica, t. 266, *O. palmata pratensis latifolia longis calcaribus* (1767), said to be common in meadows of Denmark and Norway, which well depicts the modern ' *O. incarnata* '. Against *O. sambucina* Linnaeus has written ' it. oel. 48 ', thus noting that in Oeland he saw this plant as well as *O. latifolia*. And against *O. incarnata* Haller's definition of no. 1280 is inscribed, with the significant remark ' Forte praecedentis [*O. sambucina*] varietas '.

Linnaeus's last notes on these plants are in the ' Mantissa Plantarum altera ' (1771). On page 486 we read :—

' *O. latifolia*.

O. rad. palmatis, caule fistuloso, bracteis maximis, labello trifido serrato, medio segmento obtuso. Hall. 1279, t. 32. [This is followed by five of Haller's synonyms not previously cited by Linnaeus.]
Flores spicati. Petala lateralia reflexa. Labium lateribus reflexum, 3-lobum. Calcar conicum. Bracteis flore longioribus ; foliis immaculatis. Caule fistuloso ab *O. maculata* evidens.

O. incarnata.

O. rad. palmatis, bracteis coloratis, labello circumserrato trilobo, lobo medio emarginato. Hall. 1280.
Varietas forte proximae [*O. sambucina*].

O. sambucina.

O. rad. palmatis, bracteis coloratis, labello circumserrato trilobo, lobo medio emarginato. Hall, 1280.
O. palmata lutea, labio floris maculato. Seguier Veron. 249, t. 8, f. 5.
Flores spicati, rariores, lutei. Petala lateralia reflexa. Labium lateribus reflexum, serratum, 3-lobum, medio emarginato, purpureo-maculatum. Calcar emarginatum mediocre.'

From the tenour of these notes it would appear that Linnaeus wished to disarm Haller's criticisms. He was evidently conscious that, in adding Haller's no. 1279 to the synonyms of his *O. latifolia*, he was admitting a plant illustrated by a figure showing spotted foliage, and hence, it may be judged, he embodied in his fresh description the clause ' foliis immaculatis ', to show that he could not recognise a spotted-leaved plant as belonging to that species. It will be seen that he curiously prints Haller's definition of no. 1280 both under *O. incarnata* and *O. sambucina*, and now cites Seguier under the latter, thus tacitly admitting their identity, although he merely says of the former ' varietas forte proximae '.

I think it has now been made sufficiently clear, not only that *O. latifolia* L. is the species that botanists generally in recent years have named *O. incarnata* L., but that *O. incarnata* L. is a plant which Linnaeus at first imperfectly understood, but subsequently became convinced was nothing more than a colour-form or variety of *O. sambucina* L., a species that he had simultaneously published with it.

TREATMENT OF MARSH ORCHIDS AFTER THE TIME OF LINNAEUS.

A fact that has been almost entirely lost to sight is that for nearly ninety years after its publication the name *O. incarnata* L. was never associated in botanical literature with the plant which we now know as such, but always with *O. sambucina* L. ; while *O. latifolia* L., probably through the addition of the synonym from Haller, was frequently extended to include plants whose foliage was spotted. Miller (Gard. Dict. ed. 8 (1768)) mentions *O. latifolia* only, with unspotted leaves. Villars (Hist. Pl. Dauph. ii, p. 36 (1787)) and Haller (Icones Plant. p. 36 (1795)) adopt the name *O. incarnata* L. in preference to *O. sambucina* L., presumably because it took precedence in actual print. Lamarck (Encycl. Méth. iv, p. 597 (1798)) has *O. sambucina* L. var. β. (*O. incarnata* L.), with the remark ' La var. β a été présentée par Linnaeus comme une espèce distincte ; tous les auteurs, tant anciens que modernes, ne l'ont regardée que comme variété . . . ' In 1799 *O. latifolia* L. seems first to have been definitely described and figured as a plant with spotted leaves in Sturm's Deutschl. Flora, Heft 7, xxi. Kops's ' Flora Batava ', i, t. 20 (1800) depicts *O. latifolia* L. as a form with narrow unspotted leaves, which is probably a luxuriant ' *O. incarnata* '. Smith's ' Flora Britannica ', iii, p. 924 (1804), describes under *O. latifolia* L. what is evidently our ' *O. incarnata* ', but without any reference to that name ; and a similar treatment obtains in Eng. Bot. no. 2308 (1811), and the ' English Flora ', iv, p. 22 (1828). Brotero (Fl. Lusit. p. 21 (1804)) states that *O. latifolia* L. has unspotted leaves, and gives, as a synonym of *O. sambucina* L., 'An *O. incarnata* Vill. Pl. Delph ? '

The fourth edition of ' Species Plantarum ', by Willdenow (iv, p. 28 (1805)), remarks of *O. latifolia* L. 'foliis parum maculatis . . . ab *O. maculata* . . . differt ', and (p. 30) places *O. incarnata* L. next to *O. sambucina* L., stating that it is perhaps a variety, differing only in its acute petals. Loiseleur (Fl. Gallica, ii, p. 606 (1807)) simply places *O. incarnata* L. as a var. β of *O. sambucina* L., a treatment repeated in Lamarck and De Candolle's Fl. Française, ii, p. 251, (1815), in which work a variety β (foliis maculatis) is introduced under *O. latifolia* L. Wahlenberg in Fl. Suecica, i, p. 554 (1824), as well as in its second edition (1833), likewise makes *O. incarnata* L. a var. β of *O. sambucina* L. We also get in Sprengel's Syst. Veg. ed. 16, p. 688 (1826) ' *O. sambucina* L. . . . (*O. incarnata* L. var.) '.

In 1828 the elder Reichenbach (Icon. Botan. s. Plantae Criticae) separated from *O. latifolia* L. the spotted-leaved Marsh Orchid of Central Europe under the name of *O. majalis* Reichb. At the same time he gave a contrasting account of *O. latifolia* L. (no. 1064), with a concise description, including ' labello arcubus binis maculisque signato ', and a citation in synonymy of L. Sp. Pl. 1334, Wahlb. Suec. ii, 554, and Fl. Dan. 266. Reichenbach's figure is readily recognisable as modern ' *O. incarnata* '. *O. majalis* (no. 1065) is described ' Tuberibus flexuoso-palmatis, caule angustissime fistuloso, foliis plerumque maculatis ovali-lanceolatis patentibus, bracteis flore longioribus, calcare conico germine breviori, labello orbiculato trifido crenulato, petalis lateralibus

reversis ', and *O. latifolia* Sturm, Deutschl. Fl., is quoted in synonymy. This is said to be the earliest of the group to flower. The accompanying Plate, drawn from a Dresden specimen, shows spreading, spotted, rather narrow foliage, and a broad lip, strongly lined and spotted. Reichenbach furnishes further information respecting these plants in Fl. Germ. Excurs. p. 126 (1830), mentioning that the flowers of *O. majalis* are larger than those of *O. latifolia*, and citing also Haller's figure (no. 1279, t. 32) under the former. In a continuation of Icon. Botan. (1831) Reichenbach figures *O. sambucina* L. and *O. sambucina* var. *incarnata* L. (nos. 1309 & 1310), and also (no. 1348) *O. angustifolia* Lois., first distinguished by Loiseleur (l.c.) as a variety of *O. latifolia* L., but now raised to specific rank and described from Swiss material. The figure of this new species shows a slender plant with narrow, unspotted leaves and a short, few-flowered spike of relatively large flowers.

Meanwhile the inclusion of two distinct plants under the name of *O. latifolia* L. had been noticed by Wimmer and Grabowski, who (Fl. Silesiae, ii, p. 250 (1829)) applied the Linnean name to the spotted-leaved form, and redescribed the true *O. latifolia* L. as a new species *O. angustifolia*. The relative description is a good one, and clearly indicates the modern ' *O. incarnata* ' with lined labellum. In his ' Flora von Schlesien ', p. 328 (1832), Wimmer abandons his name *O. angustifolia* for *O. incarnata* L.—the only instance of this use of the name before 1842 that I have traced,—but curiously in his second edition (1844) he reverts to his *O. angustifolia*. Dietrich (Fl. Borussica, i (1833)) similarly distinguishes two species, *O. latifolia* L. (*O. majalis* Reichb.) and *O. lanceata* Dietr. (' *O. incarnata* '). Visiani (Fl. Dalmat. i, p. 172 (1842)) uses the name *O. angustifolia* W. & G.

In 1832 Elias Fries (Novit. Fl. Suec. Mant. i, p. 16) announced that *O. incarnata* L. had been wrongly regarded as conspecific with *O. sambucina* L., and suggested that the two plants just distinguished by Reichenbach under *O. latifolia* were *O. latifolia* L. and *O. incarnata* L. Three years later, in Top. Stirp. Scan. p. 164, he identified *O. incarnata* L. with *O. angustifolia* Lois., which had been described and figured as a species in 1831 by Reichenbach. The next important work, Koch's Syn. Fl. Germ. (1837), admitted (p. 687) three species of the group under the names of *O. latifolia* L. (*O. majalis* Reichb.), *O. angustifolia* W. & G. (*O. latifolia* Reichb.), and *O. Traunsteineri* Sauter (*O. angustifolia* Reichb.), Koch remarking of *O. incarnata* L. that he had not seen a Swedish specimen, but thought it might belong to *O. Traunsteineri*. Fries followed with a fresh account of these three plants in Novit. Fl. Suec. Mant. ii, p. 53 (1839). He states here that *O. latifolia* L. (*O. majalis* Reichb.) is rare in Sweden and describes it as with leaves ' submaculata ' ; the common Swedish species is *O. angustifolia* W. & G. (*O. latifolia* Reichb.), a tall unspotted plant ; and *O. incarnata* L. (*O. Traunsteineri* Saut.), a slender unspotted form, is said to be uncommon.

In 1842, in his Herb. Norm. set of exsiccatae, no. vii, 65, Fries sent out specimens of the present-day ' *O. incarnata* ' under that name, remarking

on the labels that in another place he would demonstrate, without a shadow
of doubt, what *O. incarnata* L. really was. The other place is his 'Mantissa', iii,
published in the same year, where (pp. 127 sq.) he gives a lengthy dissertation
on the subject—which is of importance because subsequently it was generally
followed. I have repeatedly studied this paper and fail to find any solid
reason whatever for adopting its conclusions. Fries begins by recanting his
identification of *O. incarnata* with *O.Traunsteineri* Saut. (*O. angustifolia* Reichb.)
and now refers it to the commoner *O. angustifolia* W. & G. (*O. latifolia* Reichb.),
stating that from the colour of the flowers this must be correct. Continuing,
he remarks that *O. latifolia* L. is a collective species, which Linnaeus first
distinguished in Belgium, where, he says, *O. majalis* is common. I have shown
in this paper that *O. latifolia* L., excluding its varieties, is not a collective
species, but a uniform plant, with unspotted leaves, identical with our present-
day ' *O. incarnata* '; and further that the plant which Linnaeus distinguished
in Belgium (Hort. Cliff. l.c.) was not *O. majalis*, but again ' *O. incarnata* ',
the common Marsh Orchid of Sweden, which Linnaeus knew there. Fries
further states that Linnaeus's description and his var. α in Act. Upsal. point
to *O. majalis*. The description (including var. α), which is of minor importance
compared with that in Sp. Plant., is really based entirely on synonyms, all of
which refer to forms of *O. incarnata* with unspotted leaves. Another point
in Fries's paper is that all the *O. latifolia* indicated by Linnaeus himself for
Sweden is absolutely *O. sambucina*. In the first edition of Fl. Suecica, where
O. sambucina was treated as a variety of *O. latifolia*, it is not clear how far the
habitat cited refers to the species or the variety. But in the second edition,
where *O. sambucina* is separated as a species, *O. latifolia* is given as a plant of
damp mountain meadows, and ' it. oel. 48 ' is cited, showing that Linnaeus
identified with it the *O. palmata palustris, non maculata*, which he had found
at Rella. He did not cite ' it. oel. 48 ' under *O. sambucina* in this work, but
subsequently he observed the omission and added it in MS. in his copy of
Sp. Plant. ed. 2, so that the occurrence of both species in Oeland is duly noted.
Fries finally invokes the authority of the fathers in support of his contention
that *O. latifolia* L. is *O. majalis* Reichb., but he says nothing to indicate that
he had consulted any of these early authors. It is sufficient to recall that the
Marsh Orchid of the fathers, as already shown in this paper, was a plant with
unspotted leaves, and that *O. majalis* was unknown until described by Haller,
the contemporary of Linnaeus. Fries concludes his paper with an enumeration
of all the Marsh Orchids known to him, and these he divides into two classes :—
the first, southern forms, with leaves narrowed below and flowers typically
purple ; and, secondly, northern forms, with leaves narrowed from the base
upwards and flowers typically flesh-coloured. This classification suggests
a better knowledge of the plants themselves than of their history and nomen-
clature. Of the specimens sent out in Herb. Norm., no. 65 is the typical form
of ' *O. incarnata* ' like the Rella plant ; no. 66, labelled ' *O. incarnata* L. v. *alba* '
is a stronger from resembling var. *ochroleuca* Boll ; no. 67, labelled ' *O. lati-*

folia L.', is a tall plant, with narrow, lanceolate leaves, differing little from
no. 66 (as represented at Kew and in Herb. Mus. Brit.) except in its larger
flowers. So far as can be judged, it has not the aspect of *O. majalis* Reichb.

This paper of Fries has been criticised at some length because, presumably
owing to its author's reputation and his position as successor to Linnaeus at
Upsala, it has resulted in an erroneus application of Linnean names that had
previously been correctly used. It reveals no real investigation of the works
of Linnaeus, nor any knowledge of pre-Linnean literature, and has the appear-
ance of having been largely inspired by a practical desire to designate the
plants in question with appropriate epithets, viz. : *latifolia* for the broader-
leaved plant, and *incarnata* for that with flesh-coloured flowers.

As an immediate result of Fries's paper Koch, in the second edition of
Syn. Fl. Germ. p. 793 (1844), substituted ' *O. incarnata* L. Fl. Suec. 312, S. P.
1335, sec. cl. Fries ' for *O. angustifolia* W. & G. Kittel, however, in the second
edition of his Taschenbuch Fl. Deutschlands, published the same year, retained
(p. 170) *O. incarnata* under *O. sambucina*.

Fries's transfer of *O. incarnata* from *O. sambucina* to *O. latifolia* was adopted
by the younger Reichenbach in his account of the orchids in Icones Fl. Germ.
et Helvet., v. xiii (1851). In doing this Reichenbach evidently felt that some
explanation was required, for (p. 54) he says that men capable of dealing with
critical plants were still in doubt, and some would deny that *O. incarnata*
differed from *O. latifolia*. He therefore recalls the three species found at Rella
by Linnaeus and recapitulates the descriptions in Fl. ˋSuec., ed. 2, from which,
without any further references, he sets forth three conclusions, which do not
seem in any way relevant to the identification of *O. incarnata* L., and prove
that he did not make any serious attempt to justify his nomenclature. Reichen-
bach's taxonomic arrangement of the group largely coincides with that pro-
posed by Fries, but with all the forms classified under two full species only,
viz. : *O. incarnata* L. and *O. latifolia* L. Under *O. incarnata* he places as
var. *foliosa* the *O. foliosa* Solander from Madeira ; as var. *angustifolia*, *O. Traun-
steineri* Saut. ; as var. *brevicalcarata*, subvar. *rhombeilabia cruenta*, the boreal
plant, *O. cruenta* Müll. ; and under var. *sesquipedales* [sic] the Spanish *O. sesqui-
pedalis* Willd. and a kindred Algerian form. The plate of Fl. Danica 266 is
cited under a subvariety of var. *brevicalcarata* known from Russia and Persia !
O. latifolia L. is similarly subdivided. There are subvarieties *genuina* (*O. majalis*
Reichb.) and *lapponica* (*O. lapponica* Laest.) ; and varieties *subincarnata* from
China, *elata* from Algeria, *foliosa* from Madeira, *Beeringiana* from Kamtschatka,
and *conica* (*O. cordigera* Fr.). This Benthamian treatment would no longer
meet with general acceptance.

The action of the younger Reichenbach in supporting Fries's identification
of *O. incarnata* L. with *O. latifolia* L. rather than *O. sambucina* L. led to this
arrangement being generally followed by succeeding botanists. In France
Grenier and Godron (Fl. France, iii, p. 295 (1855–56)) adopted the name *O. latifolia*
for a plant with deep purple flowers and leaves usually spotted, and ' *O. incarnata*

L. . . . Fries ', Mant. iii, for the true *O. latifolia*. A similar treatment appears
in Parlatore's ' Flora Italiana ', iii, p. 251 (1858), and in Willkomm and Lange's
' Flora Hispanica ', i, p. 744 (1863). Syme, in the third edition of ' English
Botany ', ix, p. 100 (1869), writes ' *O. incarnata* Linn. Fries ' for E. B. 2308,
and ' *O. latifolia* Linn. Fries ' for the spotted-leaved plant. In other important
Floras, as well as in the recent Continental Monographs, *O. latifolia* L. repre-
sents *O. majalis* Reichb., and the original identity of *O. incarnata* L., about
which practically all writers prior to Fries were in agreement, is not even
indicated ; and in preparing this paper I have laboriously discovered what was
common knowledge to the botanists of a century ago.

MODERN TAXONOMY OF THE GROUP.

The examination of herbarium material clearly shows that throughout
the Palaearctic Region the Marsh Orchids form a polymorphic group, and that
many different forms occur, some perhaps of hybrid origin, in various parts of
their geographical range. The degree of differentiation in these forms is often
slight and it is consequently difficult to assess their taxonomic rank. But,
on the whole, when a form shows no clear affinity with any particular one of its
allies and cannot be suspected of direct hybrid origin, and when, moreover,
this form possesses a definite geographical distribution, then I think that,
in a group of polymorphs, it may well be treated as a species. Such forms are
the British *O. praetermissa* Dr. and *O. purpurella* Steph., which are really of
a status comparable with some of the subspecies and races of Continental
authors. The Marsh Orchids of Great Britain have lately been so intensively
studied in the field that perhaps no further distinct forms will be discovered,
but I suspect that in Asia, and some parts of Europe, such as Spain and perhaps
elsewhere, further forms are yet awaiting distinction.

A leading difficulty in dealing with these plants, as with other Petaloid
Monocotyledons, is the obliteration of characters in exsiccatae, which has
sometimes caused botanists with a good knowledge of the Orchids of their
own country to fall into serious errors over foreign forms. The curvature
of the perianth-segments and the labellum is invariably lost in dried specimens,
and the leaf-spots, if present, as well as the colour and markings of the flowers,
are very fugitive and frequently disappear within a few years even in the best
and most carefully dried specimens. Occasionally, however, they inexplicably
do not fade, and there is an example of *O. maculata* in the Sloane Herbarium
in which the leaf-spots are still visible ! These considerations induce me largely
to confine my attention to plants that I have seen in the living state. Good
figures, especially when well coloured, are of the greatest value, but unfortunately
plates, even the most recent, often fall far short of the desired standard.

Of the numerous works specially devoted to European Orchids which have
appeared during the last forty years, the earliest is E. G. Camus's ' Monographie
des Orchidées de France ' (1893). Here Camus (p. 46) admits two species only

of Marsh Orchids, ' *O. incarnata* L.', with three races, *O. angustifolia* Reichb., *O. sesquipedalis* Willd., and *O. integrata* Camus; and ' *O. latifolia* L.', with a race *O. foliosa* Solander. It is by no means clear what Camus intends by ' *O. incarnata* ', for he says that it has larger flowers than ' *O. latifolia* ' and flowers twenty days later. There is a specimen in Herb. Mus. Brit., labelled by him ' *O. incarnata* L. vrai! Presles. E. G. Camus. 6/91 ', which is almost certainly *O. praetermissa* Dr.; and it would appear from the descriptions and distribution that his ' *O. incarnata* ' is *O. praetermissa*, and his race *O. angustifolia* (said to be the commoner plant) ' *O. incarnata* '.

A similar doubt respecting the precise determination of ' *O. incarnata* ' may be noticed in M. Schulze's ' Die Orchidaceen Deutschlands ' (1894), for the coloured plate, quite a good one, recalls *O. praetermissa*, as does also the description of the lip—' Lippe flach oder nur schwach konvex . . . mit . . . unregelmässiger und oft punktierter Zeichnung '. This points to the possibility of *O. praetermissa* occurring in western Germany and being confused there with ' *O. incarnata* '—a possibility strengthened by the existence of German exsiccatae in herbaria apparently identical with the former species. Schulze adopts the varieties of H. G. Reichenbach under ' *O. incarnata* ', adding var. *serotina* Haussk. and a new variety *Drudei*. His next species is *O. Traunsteineri* Saut., of which he figures two forms that have the aspect of distinct species. ' *O. latifolia* L.' follows, with a good figure of a large-flowered plant with broad spotted leaves; four varieties of this are given, two of which are taken from the younger Reichenbach.

In 1898–99 another account of the Marsh Orchids, under the subgeneric name *Dactylorchis*, was published by J. Klinge in Act. Hort. Petrop. xvii. This paper deals largely with the forms of *O. Traunsteineri*, which is a prevalent and variable species in Russia, and is elaborately subdivided by Klinge. The variety *serotina* Haussk. of ' *O. incarnata* ' was raised to specific rank in 1901 by A. Schwarz (Fl. Nürnberg, iv, p. 1112), who regarded it as an intermediate between ' *O. incarnata* ' and *O. Traunsteineri*.

The third volume of Ascherson and Graebner's ' Synopsis der Mitteleuropäischen Flora ', in which the *Orchidaceae* are dealt with, appeared in 1907, and the Marsh Orchids of Central Europe are perhaps more satisfactorily treated here than in any other work, despite the authors' cumbrous system of classification. The mistakes of the younger Reichenbach's arrangement are freely corrected. The first species is *O. incarnatus* [sic], which is stated to have a flat or nearly flat lip, speckled with dark purple, as in M. Schulze's description. The species is divided into races, viz. :—*lanceatus* (*O. lanceata* Dietr.), with several varieties; *serotinus* (*O. serotinus* Schwarz); *Drudei* (*O. incarnata* v. *Drudei* Schulze); *ochroleucus* (*O. incarnata* β *ochroleuca* Boll); and *sublatifolius* (*O. incarnata* 2. *sublatifoliatae* Reichb. f.); and *O. cruentus* (*O. cruenta* Müll.) appears as a subspecies, with a race *Seemenii*. *O. Traunsteineri* Saut. is the next species. This has five races, under which are numerous varieties. The races are *Eu-Traunsteineri* (*O. angustifolia* Reichb.); *Nylanderi* (*O. latifolia* v. *angustifolia*

F. Nyl.) ; *recurvus* (*O. angustifolia* v. *recurva* Klinge) ; *Russowii* (*O. angusti-folia* v. *Russowii* Klinge) ; and *curvifolius* (*O. curvifolia* Nyl.). The succeeding species is *O. latifolius* [sic], divided into five races, *majalis* (*O. majalis* Reichb.) ; *pinguis* ; *impudicus* (*O. impudica* Crantz ?) ; *brevifolius* ; and *dunensis* (*O. latifolia* v. *dunensis* Reichb. f.). Several varieties are inserted under the races. The last species is *O. cordiger*(*O. cordigera* Fr.), with three races, viz. :— *rivularis* (*O. rivularis* Heuff.), with four varieties ; *Griesbachii* (*O. Griesbachii* Pantocs.) ; and *Rochelii* (*O. latifolia* v. *Rochelii* Gris. & Schenk ; *O. bosniaca* Beck). The very numerous forms of central Europe are brought together in as natural a sequence as is probably practicable. It may be noticed that *O. praetermissa* Dr. does not seem to be distinguished, although the allusion to the flat lip under *O. incarnatus* may point to its inclusion under that species. A rare variety *subfoliosus* of the race *lanceatus*, with undivided labellum, broader than long, may possibly be *O. praetermissa*. This species also seems allied to *O. Traunsteineri*, race *Nylanderi*, which, so far as can be seen from the exsiccata 'Dörfler, Hb. Norm. 3197 ', from Ahlbeck, closely resembles *O. praeter-missa*.

The treatment of these plants in Rouy's ' Flore de France ', xiii, pp. 148 sq. (1912), calls for little comment. Three species are admitted, *O. incarnatus* L. [sic], *O. Traunsteineri* Saut., and *O. latifolius* L. [sic], the last with a race *O. sesquipedalis* Willd., representing the tall, floriferous forms of south-west Europe that are not dealt with in this paper.

It was just after the appearance of Rouy's work on these plants that British botanists showed a revived interest in the group, as already narrated. The *O. latifolia* L., described by Smith in ' Flora Britannica ' and his subsequent works, was, of course, ' *O. incarnata* ', and though the correct plant was figured, there is little doubt but that *O. praetermissa* Dr. was confused with it and was equally identified with *O. latifolia* by our botanists. In 1863, in E.B. Suppl. 2973, Babington, following Fries, identified the *O. latifolia* of E.B. 2308 with *O. incarnata* L. and described a fresh plant with spotted foliage as *O. latifolia* L. Babington's description was drawn up from broad-leaved specimens collected at Triplow, Cambs., which appear from the figure to differ essentially from the form identified with *O. latifolia* by Godfery and the Stephensons. No similar examples have been recently collected, so far as is known. This identification of Babington's was only partially followed in England, and after C. B. Clarke (Journ. Linn. Soc., Bot., xix. p. 207 (1882)) had demonstrated which form agreed with the specimen of *O. incarnata* in the Linnean Herbarium, many British botanists continued to regard as *O. latifolia* L. the plant with unspotted leaves which was distinguished by Druce as *O. praetermissa* (Report B. E. C. iii, 5, 340 (1914)).

The characters of *O. praetermissa*, and its generic affinities, were dealt with in Journ. Bot. lxi, pp. 65 sq. (1923), and l.c. lxiii, p. 96 (1925), by Messrs. Stephenson, who regard it as approaching the south-western group of *O. ses-quipedalis* Willd.

The second new British species, *O. purpurella* Steph., first described in 1920

and figured in 1922 (Journ. Bot. pl. 562), would probably have been treated by Ascherson and Graebner as a race of ' *O. latifolia* ' (*O. majalis* Reichb.), from which it differs little except in its normally subentire lip.

The two new British species, *O. praetermissa* Dr. and *O. purpurella* Steph., are admitted as such in Keller and Schlechter's Mon. & Icon. der Orchideen Europas &c. (1927). Very few varieties in the genus *Orchis* are distinguished in this work, and diagrams of enlarged flowers only have so far been published.

In 1927 another exhaustive and interesting account of the Section *Dactylorchis* by Fuchs and Ziegenspeck was printed in Bot. Archiv. xix, pp. 163 sq. This work deals largely with the morphology of the group, and gives enlarged figures of the seeds of different forms. The authors find, as Mr. Dymes has done in this country, that the seeds do not afford very definite taxonomic characters.

The ' Iconographie des Orchidées d'Europe ' appeared in 1928-29—an elaboration of a monograph written by E. G. Camus in 1908 and now completed by his daughter, Mlle A. Camus. This is the most complete existing monograph of the family. Among the Dactylorchids *O. cordigera* is divided into seven varieties. *O. praetermissa* Dr. and its varieties are adopted, and it is said to bloom ten to fifteen days after ' *O. incarnata* ', which in its turn is given as flowering at least twenty days later than ' *O. latifolia* '. *O. integrata* Camus becomes a subspecies of *O. praetermissa*. ' *O. incarnata* L.' is divided into thirteen varieties, and a subspecies, *O. lanceata* (Dietr.) is added. *O. cruenta* Müll. is treated as a full species. *O. angustifolia* Lois. ap. Reichb. is the next species, with six varieties and a subspecies *O. curvifolia* (Nyl.). A footnote draws attention to the work of Fuchs and Ziegenspeck, who consider this species to be an agglomeration of hybrids. ' *O. latifolia* L.' has eight varieties and a subspecies *O. baltica* (Klinge), and is followed by *O. purpurella* Steph. A copious synonymy is usually furnished for each species, but some important early works are omitted. A few citations are open to criticism. *O. incarnata* Willd., shown under ' *O. incarnata* L.', would be better referred to *O. sambucina* L., and *O. latifolia* Willd. more properly belongs to ' *O. incarnata* L.' Among the Icones, Vaillant, t. 31, ff. 1–5, and Fl. Dan. 266 are both cited under ' *O. latifolia* ' instead of ' *O. incarnata* '; and Vaillant, t. 30, ff. 14, 15, which is cited under ' *O. incarnata* ', is nearer to *O. praetermissa*. The same figure from Seguier's ' Plantae Veronenses ' is quoted both under *O. sambucina* and ' *O. incarnata* '. The plates of this important work show little detail and are crudely coloured.

A recent work that merits notice owing to the conspicuous excellence of its plates is E. Nelson's ' Die Orchideen Deutschlands ' (text by Dr. Hermann Fischer), which was published in 1931.

The treatment of the Dactylorchids in Col. Godfery's ' Monograph and Iconograph of Native British Orchidaceae ' (1933) leaves much to be desired. ' *O. incarnata* ' is shown with var. *pulchella* Dr. and var. *dunensis* Dr., to which are added a var. *albiflora* and a form *atrirubra*. Under *O. praetermissa* Dr. the variety *pulchella* Dr. is retained, with var. *macrantha* Sipkes. ' *O. latifolia* '

is described with one variety, *eborensis*—' The Mystery Orchid ',—which is printed apart after *O. purpurella* Steph., and no British stations are mentioned, although the species is stated to be widely distributed. As the most controversial of the British Marsh Orchids, it might have been expected to be adequately figured, but it is represented only by a spike of flowers on a plate illustrating *O. maculata*. There is some confusion in this plate, for the foliage depicted does not look like that of any form of *O. maculata*. The citation of synonyms, icones, and exsiccatae is almost dispensed with throughout, and the names of the new groups are invalidated through the absence of Latin diagnoses*.

An interesting account of the Dutch Marsh Orchids with spotted foliage, by P. Vermeulen, was published last year (1933) in Ned. Kruidk. Archief. pp. 397 sq., and subsequently in Journ. Bot. (lxxii, p. 97).

CONCLUSION.

I will conclude this paper with a synopsis of the British forms and a few others with which I am familiar on the Continent, using the revised nomenclature necessitated by the reversion to the original Linnean names. Synonyms, a few exsiccatae, and, particularly, figures will be cited whenever they appear free from any element of doubt. As these plants have been so fully described in the recent Monographs &c., diagnoses, with the salient features only, will usually be given.

The measurements in the following descriptions are taken from dried material unless the contrary is stated. The sign ! indicates that I have collected the plant *in situ*. Plants of which I have seen dried specimens only are placed in square brackets and marked ' v.s.' (vidi siccum).

ORCHIS Linn.

Sect. *Androrchis* Endl.   Subsect. *Latifoliae* Reichb. f. (*Dactylorchis* Klinge).

I. Tubers deeply lobed or palmate.

a. *Latifoliae verae.*   Flowers normally small. Labellum as long as broad, or longer (rarely shorter).

 1. *O. latifolia* L.   Plant dwarf to tall. Leaves unspotted, narrowed from the base upwards.

 2. *O. cruenta* Müll.   Plant dwarf. Leaves spotted on both sides, contracted at the base.

b. *Subsesquipedales.*   Flowers rather large. Labellum broader than long. Leaves long and narrow, broadest near the base. Normally tall plants.

 3. *O. praetermissa* Druce.   Leaves unspotted. Labellum speckled.

 4. *O. pardalina* Pugsl.   Leaves spotted above. Labellum lined.

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* The International Congress at Cambridge in 1930 extended the recognition of new groups published without a Latin diagnosis from 1908 to January 1, 1932. The date shown in the recently issued abridgement of the Rules is January 1, 1935.

c. *Majales*. Labellum broader than long. Leaves usually spotted above, ±contracted towards the base.

5. *O. purpurella* Steph. Plant ±dwarf. Leaves typically slightly spotted. Flowers of moderate size.

6. *O. majalis* Reichb. Plant dwarf to rather tall. Leaves distinctly spotted. Flowers rather large.

7. *O. alpestris* Pugsl. Plant rather dwarf. Leaves broad, heavily spotted. Flowers large.

II. Tubers shortly 2–3-lobed.

8. *O. sambucina* L. Plant dwarf. Leaves unspotted. Flowers large, yellow, reddish, purple, or flesh-coloured.

I a. LATIFOLIAE VERAE.

1. ORCHIS LATIFOLIA L. Sp. Plant. 941, excl. var. δ (1753) ; Fl. Suec. ed. 2, 312 (1755) ; Sp. Pl. ed. 2, 1334 (1763) ; Mantissa alt. 486 (1771) ; Miller, Gard Dict. ed. 8 (1768) ; Scopoli, Fl. Carniol. ii. 197 (1772) ; Curtis, Fl. Lond. 5, t. 65 (1788) ; Lamk. Encycl. Méth.* iv, 596 (1798) ; Kops, Fl. Batav.* t. 20 (1800) ; Smith, Fl. Brit. iii, 924 (1804) ; Brotero, Fl. Lusit. 21 (1804) ; Willd. Sp. Pl.* ed. 4, iv, 28 (1805) ; Lois. Fl. Gallica, ii, 606 (1807) ; Smith, Eng. Bot. no. 2308 (1811) ; Lamk. & DC. Fl. Franç.* iii, 251 (1815); Wahlb. Fl. Suecica, i, 554 (1824) ; Sprengel, Syst. Veg.* ed. 16, 687 (1826) ; Smith, Eng. Flora, iv, 22 (1828) ; Reichb. Icon. Botan. no. 1064 (1828) ; Fl. Germ. Excurs. 126 (1830). *O. angustifolia* Wimm. & Grab. Fl. Siles. ii, 252 (1829). *O. lanceata* Dietr. Fl. Boruss. i, t. 5 (1833). *O. incarnata* Fries, Mant. iii, 127 (1842) ; Reichb. f. Icon. Fl. Germ. xiii, 51 (1851) ; M. Schulze, Orchid. Deutschl. no. 19 (1894) ; Asch. & Graebn. Syn. Mitteleur. Fl. iii, 715 (1907) ; Rouy, Fl. Fr. xiii, 148 (1912) ; Stephenson in Journ. Bot. lxi, 273 (1923) ; E. G. & A. Camus, Icon. Orchid. d'Europe, i, 222 (1928) ; Godfery, Mon. Brit. Orchid. 185 (1933) ; et mult. auct. recent. ; non *O. incarnata* Linn. [Pl. 31.]

Satyrium basilicum primum (*vel mas*), Dod. Fl. Coron. 216 (1568). *Palma Christi et Serapias mas laevi folio*, Lobel, Stirp. Hist. 91 (1576). *Orchis palmata pratensis latifolia, longis calcaribus*, C. Bauh. Pin. 85 (1623) ; Morison, Hist. iii, 498 (1699) ; Tourn. Inst. i, 434 (1700) ; Rudbeck, Camp. Elys. 211 (1701) ; Boerhave, Pl. Lugd. 152 (1720) ; Ray, Syn. ed. 3, 380 (1724) ; Vaillant, Bot. Par. 152 (1727). *Palmata non maculata*, J. Bauh. Hist. ii, 774 (1651) ; Ray, Hist. ii, 1223 (1688).

Icones. Vaillant, l.c. pl. 31, ff. 1–5 ; Fl. Dan. 266 ; Eng. Bot. 2308 ; Reichb. l.c. f. 769 ; Dietrich, l.c. t. 5, as *O. lanceata*; Reichb. f. l.c. t. 397, as *O. incarnata*; Barla, Icon. Pl. 50, central fig., as *O. incarnata* ; Journ. Linn. Soc., Bot., xix, pl. 31, as *O. incarnata* ; Journ. Bot. pl. 556, ff. 1 & 24, & pl. 569, as *O. incarnata* ;

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* In these works the species includes plants with spotted leaves, sometimes separated as varieties.

Butcher & Strudwick, Further Illustr. f. 348, as *O. incarnata*; Fischer & Nelson, Orchid. Deutschl. pl. 5, f. 11, as *O. incarnata* ; Godfery, l.c. pl. 43, as *O. incarnata*.

Exsicc. Reichb. no. 1135 ; Fries, Hb. Norm. vii, 65, as *O. incarnata* ; Edwards, Rella, Oeland, 1922, in Hb. Mus. Brit. ; Fl. Ingrica no. 630 ; Magnier no. 1808, as *O. Traunsteineri* ; Soc. Dauph. no. 445 bis, as *O. incarnata*.

Plant usually 15–30 (rarely 50) cm. high, with fistular stem and loose leaf-sheaths. Leaves ±erect, narrowed almost from the base, long lanceolate, unspotted. Spike dense-flowered, with bracts, at least the lower, exceeding the flowers. Flowers small, in colour salmon-pink (flesh-coloured) or reddish purple, rarely purple, straw-coloured, or white ; lateral sepals usually spotted ; lip 5–7 mm. long, 4–7 mm. broad, obovate or rhomboidal, and obscurely 3-lobed with the central lobe longest, marked with ±continuous lines and spots, the sides laterally reflexed almost from opening.

β. *Gemmana*, var. nov.

O. latifolia var. *β*, L. ll.c.

Serapias palustris latifolia flore albo subpurpurascente praecocior Lobel, Hist. 91 (1576). *O. palmata palustris latifolia* C. Bauh. Pin. 86 (1623).

Icones. Lobel, l.c. ; Curtis, l.c. ; Kops, l.c.

Exsicc. Herb. Sloane 40/18, *O. palmata palustris latifolia*, labelled by Vaillant (type) ; Schultz, Hb. Norm. 1244, in Hb. Manchester, as *O. incarnata* ; Preusse, Stassfurt, 1879, in Hb. Manchester, as *O. incarnata* ; Larsson, Pl. Scand. Gotland, 1892, in Hb. Mus. Brit., as *O. incarnata* ; Jage, Sorge, Cölleda, 1881, in Hb. Manchester, as *O. incarnata* ; Marshall, no. 3692, as *O. incarnata* ; Irvine, Minster, in Hb. Kew., as *O. incarnata* ; Formanek, Fl. Moravica, Altenmarkt, in Hb. Kew., as *O. incarnata*: Pugsley, no. 505.

Planta elatior, usque ad 1 m. ; folia saepius longissima ; spica longa, multiflora, bracteis plerumque quam floribus multo longioribus praedita. Aliter ut in typo.

Plant tall, up to 1 m. high ; leaves usually very long ; spike long, many-flowered, with nearly all the bracts much longer than the flowers.

[γ. *ochroleuca* (Boll), comb. nov.

O. ochroleuca Schur, Enum. Pl. Transs. 641 (1866). *O. incarnatus* race *ochroleucus* Asch. & Graebn. l.c. 719 (1907).

Icon. Fischer & Nelson, l.c. pl. 5, f. 12.

Exsicc. Heiland, Obersee, Lychen, 1880, in Hb. Manchester; Meyer, Meseritz, Posen, 1885, in Hb. Mus. Brit.

Plant tall, up to 50 cm. Flowers straw-coloured with yellowish lip. v.s.]

δ. *pulchella* (Druce), comb. nov.

O. incarnata var. *pulchella* Dr. in Report B. E. C. v, 167 (1918) ; Godfery, l.c. 187 (1933).

Exsicc. Stephenson, New Forest, 1923, in Hb. Mus. Brit. & Hb. Kew. ; Pugsley, no. 506 ; Trimen, New Forest, 1864, in Hb. Mus. Brit.

Flowers larger than in the type, bright reddish purple, with subentire lip, 8 mm. long and 7–8 mm. broad, strongly variegated with darker lines and but little laterally reflexed.

ε. *coccinea,* var. nov.

O. incarnata f. *atrirubra* Godfery, l.c. 187– nomen.

Icones. Godfery, l.c. pl. 44 ; Journ. Bot. pl. 556, f. 4.

Exsicc. Pugsley, no. 507 (Whitford).

Planta vulgo satis nana, foliis supremis spicam interdum superantibus. Flores coccinei (in sicco atro-rubentes), labello quam typi minus maculato et minus lateribus reflexo.

Plant usually rather dwarf, with upper leaves sometimes exceeding the spike. Flowers bright, clear crimson-red (becoming maroon in dried specimens), with lip less marked and less laterally reflexed than in the type.

ζ. *cambrica,* var. nov.

O. Traunsteineri Druce in Report B. E. C. iv, 212 (1916), non Saut., nec aliorum.

Icon. Journ. Bot. pl. 556, f. 2.

Exsicc. Pugsley, no. 508 (Borth).

Planta satis nana, ad 20 cm. alta. Flores purpurei, labello brevi (5–6 mm. longo latoque) vix trilobato sepala lateralia obtusa subaequante et cornu crasso quam ovario duplo breviore praediti.

Plant rather dwarf, up to 20 cm. high. Flowers purple, with short (5–6 mm. long and broad), scarcely lobed lip subequalling the blunt, faintly spotted lateral sepals. Spur short, thick, about half as long as the ovary.

This species, originally noticed by Dodoens and the first of the group to be described by Linnaeus, has the widest geographical distribution of all the Marsh Orchids and is eminently variable. It has become customary to regard the form with pale salmon-pink or flesh-coloured flowers as the typical species, owing to this colour agreeing with the specific epithet ' *incarnata* ', but the flowers are often bright reddish purple (in this country chiefly in Scotland), and Linnaeus may have had such a plant in mind when he contrasted the ' floribus rubris' of *O. latifolia* with the pale-flowered ' *O. incarnata* ' in ' Flora Suecica ', ed. 2. In Mr. Edwards's specimens from Rella the flowers seem to have been reddish.

The variety *Gemmana,* as originally figured by Lobel, is the one form of the group distinguished by Cornelius Gemma which is really recognisable ; and, as a marsh plant widely spread over Europe, it seems worthy of varietal distinction. In Britain it is much less common than the typical species and occurs chiefly in the marshes of south-east England.

Godfery's form *atrirubra* has been raised to varietal rank (var. *coccinea*) on account of the remarkable colour—almost scarlet—of its flowers, and may

repay closer examination. It grows with the dune-form of the typical species
in several maritime stations in South Wales and is perhaps endemic.

My specimens of var. *cambrica* were collected in 1905 at Borth, in Cardigan-
shire, and in colour of flower much resemble *O. praetermissa*. Messrs. Stephenson
(Journ. Bot. lxi, 277) refer to this plant as characteristic of Borth and Tregaron
bogs.

Druce's variety *dunensis* (Report B. E. C. iv, 3, 212 (1916)) appears to be
a state due to environment ; and *O. incarnata* var. *albiflora* Godfery (l.c. 187)
is probably an albino.

2. O. CRUENTA Müller, Fl. Danica, t. 876 (1782) ; Willd. Sp. Pl. ed. 4, iv,
29 (1805) ; Keller & Schlechter, Mon. Orchid. Europas, 168 (1927) ; E. G. & A.
Camus, Icon. Orchid. d'Europe, 226 (1928). *O. incarnatus* subsp. *cruentus* Asch.
& Graebn. Syn. Mitteleur. Fl. iii, 720 (1907). *O. haematodes* Reichb. Fl. Germ.
Excurs. 126 (1830) ?

Icones. Fl. Dan. t. 876 ; Reichb. f. Icon. Fl. Germ. xiii, t. 395, f. 1.

Exsicc. Schultz, Hb. Norm. 2592 ; Warodell, Fröson, Jemtland, 1881 ;
Pugsley, nos. 509 & 510.

Stem about 20 cm. high, very fistular. Leaves erect-spreading, oblong-
lanceolate (the longest about 8 cm. long), acute, broadest a little below the
middle and narrowed downwards to close stem-sheaths, densely spotted on both
sides with small, dark reddish spots. Spike dense ; bracts spreading-incurved,
the lower much exceeding the flowers, heavily spotted and suffused with
purplish red. Flowers rather small, purple ; lateral sepals reflexed, faintly
spotted ; lip about 6 mm. long and broad, obovate or rhomboidal, subentire
or obscurely 3-lobed with the central lobe longest, with numerous darker lines
and markings, laterally reflexed ; spur cylindric-conic, shorter than the purple-
tinted ovary.

The above short description has been drawn up from specimens which I col-
lected last summer (1933) in a small alpine marsh above Findelen, Zermatt,
at an altitude of about 8000 ft. The examples differ very little from Scandi-
navian exsiccatae, so far as can be judged from dried material, and closely
match the original figure in ' Flora Danica '. On comparing the Findelen
plants with others in my herbarium, I found that I had previously obtained
the same form in 1909 on damp slopes above Zmutt, near Zermatt, at a similar
altitude ; these specimens I had originally labelled ' *O. latifolia* L. var. —— '.

As *O. cruenta* thus occurs in two distinct localities near Zermatt it may be
expected to be found in other stations in the Swiss Valais. It does not appear
to have been identified hitherto as a Swiss plant, and is an interesting addition
to the list of boreal species which grow also in the Alps of Central Europe.

I *b*. SUBSESQUIPEDALES.

3. O. PRAETERMISSA Druce in Report B. E. C. iii, 5, 340 (1914) ; ib. v, 1,
149 (1918) ; Stephenson in Journ. Bot. lxi, 65 (1923) ; Keller & Schlechter,
Mon. Orchid. Europas, 176 (1927) ; E. G. & A. Camus, Mon. Orchid. d'Europe,

218 (1928) ; Godfery, Mon. Brit. Orchid. 192 (1933). *O. incarnata* E. G. Camus, Mon. Orchid. France, 46 (1893) ? *O. latifolia* and *O. incarnata* auct. angl. ex parte, non Linn.

Icones. Report, B. E. C. v, pl. 1 ; Journ. Bot. pl. 556, ff. 5–8 and pl. 566 ; Butcher & Strudwick, Further Illustr. f. 349 ; Cary Gilson, Brit. Palm. Orchids, pls. 8–10 ; Godfery, l.c. pl. 46.

Exsicc. Hb. Sloane, 312/119/1 (Uvedale) ; Druce, Radley, 1915, in Hb. Mus. Brit.; Prior, Hitchin, 1875, in Hb. Mus. Brit., as *O. latifolia*; Pugsley, no. 511 ; A. B. Jackson, Alderney, 1933, in Hb. Mus. Brit. ; E. G. Camus, Presles, 1891, in Hb. Mus. Brit., as *O. incarnata* ; Gadeceau, Finisterre, 1909, in Hb. Mus. Brit., as *O. incarnata*.

Plant usually 20–40 cm. high, but sometimes much taller (–70 cm.), with fistular stem and normally rather loose leaf-sheaths. Leaves erect-spreading, very little dilated above the base, long lanceolate, unspotted. Spike dense, often long and many-flowered, with bracts mostly exceeding the flowers. Flowers normally rather large, purple or lilac ; lateral sepals generally unspotted ; lip 6–8 mm. long, 7–12 mm. broad, nearly flat, reniform-rhomboidal, shortly 3-lobed, marked with broken lines and fine dots, not laterally reflexed until after anthesis.

O. praetermissa has been confounded in Britain with ' *O. latifolia* ' and ' *O. incarnata* ', and also in France under the latter name. It is possible that, as already explained, a similar confusion has taken place in Germany.

The species is widely distributed in England and Wales, and seems to occur also in N.E. Ireland. In Scotland it is doubtful. It is general in the Channel Islands! and is known in France from Brittany at least as far east as Paris. It grows also in Belgium and Holland (Vermeulen and Sipkes). Its occurrence in Germany is uncertain, but a few exsiccatae, such as ' Leimbach, Wattenscheid, Westfalen, 1878 ', in Herb. Manchester, and ' Schultz, no. 1151, Bitsche, Moselle ', in Herb. Kew., may perhaps belong here.

4. O. PARDALINA, sp. nov.

O. latifolia Stephenson in Journ. Bot. lix, 1 (1921) ; Godfery & Stephenson in Journ. Bot. lxii, 175 (1924) ; Butcher & Strudwick, Further Illustr. no. 350 (1930) ; Cary Gilson, Brit. Palm. Orchids, 17 (1930) ; Godfery, Mon. Brit. Orchid. 196 (1933) ? non Linn., nec aliorum. *O. latifolia* var. *junialis* Vermeulen in Ned. Kruidk. Archief. 397 (1933) ; Journ. Bot. lxxii, 97 (1934).

Icones. Journ. Bot. pl. 556, ff. 13, 14, 16 ; Butcher & Strudwick, l.c. f. 350 ; Godfery, l.c. pl. 47 B (flower-spike only) ; Cary Gilson, l.c. pls. 12–15 ; all as *O. latifolia*.

Exsicc. Pugsley, nos. 512 (Lewes) (type) and 513.

Caulis 20–50 (raro –70) cm. altus, fistulosus. Folia erecto-patentia, plerumque longe lanceolata, inferne paululum angustata et laxiusculo vaginantia, conspicue anulato-maculata. Spica densa, saepe elongata, multiflora ; bracteae inferiores solae florem superantes. Flores satis magni, pallide purpurei

vel lilacini ; sepala lateralia obscure purpureo-notata ; labellum 7–8 mm.
longum, 8–10 mm. latum, planiusculum, rhomboideo-rotundatum, leviter
3-lobatum, duobus amentis saturate purpureis maculisque numerosis notatum,
ante anthesin haud lateribus reflexum.

Tubers subpalmate. *Stem* normally tall, 20–50 (*rarely* –70) *cm. high, fistular*,
angled above. *Leaves* usually 6–7, grey-green, *erect-spreading, long lanceolate*,
acute (except the lowest, which are oblong-lanceolate, ±obtuse), *slightly
narrowed below into rather loose sheaths, conspicuously* spotted on the upper side,
usually *ring-spotted* except on the uppermost leaves. *Spike dense, elongate
and many-flowered in strong plants* ; *bracts* subulate-lanceolate, acute, *the
lowest only exceeding the flowers. Flowers rather large, light purple or lilac*,
occasionally deeper purple ; *lateral sepals* strongly reflexed, *obscurely blotched*
with darker purple ; *lip 7–8 mm. long, 8–10 mm. broad, nearly flat, rhomboid-
rotundate, shortly 3-lobed*, the lateral lobes broad and rounded, the central
narrower, rather longer, ±triangular, obtuse or subacute, the whole *marked
with 2 dark purple loops, with numerous marks* within and a few without, the
margins often slightly incurved ; *not laterally reflexed until after anthesis* ;
spur conic-cylindrical, a little shorter than the ovary. Seeds (ap. Dymes)
similar to those of *O. praetermissa*, but somewhat shorter and broader.

O. pardalina is described as a presumed species on the basis of a distinct
and fairly uniform British plant which seems identical with a form considered
by Messrs. Godfery and Stephenson to belong to ' *O. latifolia* ', but rejected
by Druce and other British botanists as a hybrid of *O. praetermissa* with
O. maculata. The plant grows in marshy fields, generally in company with
O. praetermissa, and often some form of *O. maculata* is also present. It can
hardly be disputed that hybrids of *O. praetermissa* and *O. maculata* occur,
for where the two species grow together a whole series of intermediates may
sometimes be found. But the curious ' ring ' spots and the distinct double
loop on the lip, which characterise *O. pardalina*, are not intermediate features
and would not be expected as the result of hybridity ; and according to
Mr. Dymes the plant develops perfect seeds. Moreover, it is moderately
uniform and constant in several places in the south of England ; and Vermeulen
states that it grows in Holland with *O. praetermissa*, but without *O. maculata*.
It is therefore thought desirable to treat the plant as a taxonomic species,
although in the future it may be proved experimentally to be of the hybrid
origin suggested.

From the more obvious hybrid *O. praetermissa* × *maculata* (sensu lato), with
which it probably grows at times, *O. pardalina* is distinguishable by its fewer
and larger upper leaves—indeed, except for the spots and the more glaucous
colour, its foliage is scarcely separable from that of *O. praetermissa*. Its bracts
are generally longer than in the hybrid ; and its flowers are, on an average,
darker, with a narrower, less lobed, and more distinctly lined lip, and a
thicker spur.

The new species seems most closely allied to *O. praetermissa* Dr., and it
may be seen, on referring to the tabular diagnoses in the joint paper of Messrs.

Godfery and Stephenson (l.c.) that the features of the two species nearly coincide, except that the leaves of ' *O. latifolia* ' are ring-spotted and its labellum shows a different colour and markings.

O. pardalina differs in several respects from *O. majalis* (*O. latifolia* auct. plur. recent.). It flowers with *O. praetermissa* in June and July—fully a month later than the lowland *O. majalis*. It is a taller plant, with longer, less spreading leaves, marked mainly with dark rings instead of solid spots. Its flower-spike is appreciably denser, whether in weak or strong individuals ; and the flowers are of a lighter colour, with a narrower, less deeply 3-lobed lip, which is marked with distinct dark loops rather than irregular broken lines and spots.

I have collected *O. pardalina* in two separate stations near Lewes, Sussex ; near Eashing, Surrey ; at Sandwich, Kent ; and near Icklingham, Suffolk. It also grows around Winchester, in Hants, and probably in many other localities in the south of England. It occurs also in Holland (Vermeulen) ; and perhaps likewise in northern France, where however, it may have been confused either with *O. majalis* or hybrids of *O. maculata*.

I c. MAJALES.

5. O. PURPURELLA Steph. in Journ. Bot. lviii, 164 (1920) ; Godfery & Stephenson in Journ. Bot. lxii, 175 (1924) ; Keller & Schlecter, Mon. Orchid. Europas, 174 (1927) ; E. G. & A. Camus, Icon. Orchid. d'Europe, 235 (1928) ; Stephenson in Report B. E. C. ix, 1, 203 (1930) ; Godfery, Mon. Brit. Orchid. 217 (1933).

Icones. Journ. Bot. pl. 556, ff. 9 & 10, & pl. 562 ; Cary Gilson, Brit. Palm. Orchids, pl. 11 ; Butcher & Strudwick, Further Illustr. f. 351 ; Godfery, l.c. pl. 53 A.

Exsicc. Stephenson, Aberystwyth, 1921, and Arran, 1921, in Hb. Mus. Brit. ; Wilmott, nos. 2026, 2038, & 2047 (Teesdale, 1923), as *O. latifolia*.

Plant generally about 15 cm. high, in wet ground up to 30 cm., with ±fistular stem and rather close leaf-sheaths. Leaves erect-spreading, oblong-lanceolate or lanceolate, shortly narrowed below, typically marked above with small spots especially towards the apex, but often unspotted. Spike short, dense, with lanceolate bracts scarcely exceeding the flowers. Flowers of moderate size, dark purple ; lateral sepals usually unspotted ; lip 6–7 mm. long, 7–9 mm broad, flat, rhomboidal, typically subentire, but sometimes obscurely 3-lobed, variegated with irregular, darker lines and spots ; spur conic-cylindrical, much shorter than the ovary.

β. *pulchella* (Dr.), comb. nov.

O. praetermissa var. *pulchella* Dr. in Report B. E. C. v, 5, 577 (1920) ; Stephenson in Journ. Bot. lxi, 68 (1923) ; Godfery, l.c. 194.

Exsicc. Stephenson, Arran, 1921, as *O. praetermissa* var. *pulchella* ; Wilmott, nos. 2161 & 2165, Roscobie, 1924, as *O. latifolia* ; Shoolbred, N. Uist, 1894, in Hb. Mus. Brit., as *O. latifolia*.

Plant generally taller than the type (10–35 cm.), with slenderer and less fistular stem. Leaves always unspotted. Lateral sepals frequently spotted.

O. purpurella is placed among the *Majales* as its ensemble of characters seems to approach *O. majalis* Reichb. rather than *O. praetermissa* Dr. It is essentially a smaller plant than the latter, an inhabitant of moist meadows rather than bogs and marshes ; and the form of its foliage, as well as the dark colour of its flowers, recalls *O. majalis*. It differs, however, in its late flowering—June and July, instead of May. I first collected this plant in Teesdale in June 1896, and then referred it to ' *O. latifolia* ' as a British form with slightly spotted foliage.

There appear to be some elements of confusion in Druce's account of *O. praetermissa* var. *pulchella*. The colour of its flowers is given as variable, ranging from purplish rose to dark bluish purple ; and most of the habitats cited are on the west side of Scotland or the extreme north, no station being mentioned for Perthshire. The common Marsh Orchid of Perthshire, which I first found in 1899, is a uniform plant closely matching *O. purpurella* except for its somewhat taller habit and unspotted leaves, and it always has the same dark purple flowers. An identical form is frequent in Forfarshire, and it is the only one that I have seen there. These plants agree with the Stephensons' specimens of var. *pulchella* from Arran, which they regard as scarcely distinguishable morphologically from *O. purpurella*. Near Fort William, on the west coast of Scotland, I have seen a slightly different form with flowers more like those of ordinary *O. praetermissa*, and as such plants may be widely distributed in Scotland, it is possible that Druce did not distinguish them from the Perthshire form, and regarded all of them as falling under his var. *pulchella*. As Druce clearly intended this variety *pulchella* to represent the common, dark purple Marsh Orchid of the Highlands, and as this plant, when normal, is obviously nearer to *O. purpurella* than to *O. praetermissa*, the varietal name has been transferred accordingly, but it is probable that much of the Scottish material is simply *O. purpurella* with unspotted leaves. Mr. Dymes detected a difference between the seeds of *O. purpurella* and the var. *pulchella* from Arran, which seems remarkable in view of the plants' general close affinities.

There are a number of specimens from Orkney and Shetland in Herb. Mus. Brit., labelled ' *O. latifolia* ', which appear to belong to *O. purpurella*. Messrs. Stephenson (Report B. E. C. l.c.) state that the species is frequent in Orkney, where it varies much in its leaf-spots. Some of the Museum specimens vary in the form of the labellum, which may be quite broad and distinctly three-lobed. A similar plant is ' Marshall, no. 2457 ', from Farr Bay, West Sutherland. If the definition of *O. purpurella* be extended to cover forms with fully spotted leaves and a trilobate labellum, then there will be little to separate it from *O. majalis* Reichb. except its later flowering. The dates of the Scottish specimens in Herb. Mus. Brit. range from 18th June to 13th July.

Several Irish specimens in Herb. Mus. Brit., collected in the latter half of June, also seem to be *O. purpurella*. Such are ' Miss Kinahan, Macanush

and Larganreah, Donegal, 1886 ' ; ' Britten and Nicholson, Youghal, Cork ; Newcastle, Tipperary ; and Kilmacthornas, Waterford, 1882.' The Waterford plant is stated on the label to have been named by the younger Reichenbach ' *O. latifolia* v. *brevifolia* ', but it only slightly resembles his figure in Icones Fl. Germ. and is clearly not the plant understood under this name by Ascherson and Graebner (l.c. p. 737).

6. O. MAJALIS Reichb. Icon. Botan. no. 1065 (1828) ; Fl. Germ. Excurs. 858 (1830). *O. latifolia* Sturm, Deutschl. Fl. Heft 7, xxi (1799) ; Fries, Mant. i, 16 (1832) ; Mant. iii, 127 (1842) ; Koch, Syn. Fl. Germ. 687 (1837) ; Reichb. f. Icon. Fl. Germ. xiii, 57 (1851) ; Gren. & Godr. Fl. France, iii, 295 (1855–6) ; Barla, Icon. 61 (1868) ; M. Schulze, Orchid. Deutschl. 21 (1894) ; Asch. & Graebn. Syn. Mitteleur. Fl. iii, 732 (1907) ; Rouy, Fl. France, xiii, 150 (1912) ; Keller & Schlechter, Mon. Orchid. Europas, 176 (1927) ; E. G. & A. Camus, Icon. Orchid. d'Europe, 231 (1928); non *O. latifolia* Linn. *O. latifolia* var. *majalis* Vermeulen in Journ. Bot. lxxii, 97 (1934).

O. radicibus palmatis, caule fistuloso, bracteis maximis, labello trifido serrato, medio segmento obtuso. Haller, Hist. Helv. ii. 142 (1279) (1768), ex parte.

Icones. Reichb. l.c. f. 771 ; Reichb. f. l.c. pl. 402, as *O. latifolia.*

Exsicc. Reichb. f., Heller, Dresden, in Hb. Mus. Brit. ; Traunsteiner, Kitzbühl, 1844, in Hb. Mus. Brit. ; Mortensen, Jonstrup, 1887, in Hb. Mus. Brit. ; Billot, nos. 657 & 657 bis, as *O. latifolia* ; Reverchon, Fortan, Alpes-Maritimes, 1886, in Hb. Manchester, as *O. latifolia* ; Stephenson, Logère, Cantal, 1927, in Hb. Mus. Brit., as *O. latifolia.*

Plant 10–30 (rarely –45) cm. high, with ±fistular stem and rather close leaf-sheaths. Leaves 5–7, ±spreading, oblong or lanceolate, broadest near the middle, except the uppermost, normally marked on the upper side with conspicuous solid brown spots. Spike short to fairly long, often rather lax-flowered, with lanceolate bracts mostly exceeding the flowers. Flowers rather large, deep purple ; lateral sepals slightly spotted ; lip 7–9 mm. long, 9–11 mm. broad, flat, rotund-rhomboidal, 3-lobed, the outer lobes broad, angled or rounded, the central one narrow, generally obtuse, equalling or exceeding the lateral ones, the whole lip variegated with darker lines and spots ; spur conic-cylindrical.

β. *pinguis* (Asch. & Graebn.), comb. nov.

O. latifolia race *pinguis* Asch. & Graebn. l.c. 735.

Icones. Haller, l.c. 1279, t. 32 ; Sturm, l.c. f. 21 ; Barla, l.c. pl. 48 ; M. Schulze, l.c. pl. 21 ; Journ. Bot. t. 603, as *O. latifolia* v. *majalis* ; Fischer & Nelson, Orchid. Deutschl. pl. 4, f. 9, as *O. latifolia.*

Exsicc. Reichb. no. 171.

Plant robust, somewhat elongate. Leaves shorter, broader, and often more distant than in the type, ±ovate-lanceolate, broadest below the middle. Flower-spike often rather lax.

γ. *occidentalis*, var. nov.

Exsicc. Pugsley nos. 514 (Lisdoonvarna) (type), 515, & 516.

Tubera alte palmata, segmentis saltem duobus elongatis praedita. *Caulis* 10–20 (raro –30) *cm. altus. Folia patentia, saepissime arcuato-recurvata, latiuscule lanceolata,* superiora supra basin plane dilatata, omnia vulgo valde brunneo-maculata. *Spica brevis, densiflora.* Flores saturate purpurei ; labellum 7–8 mm. longum, 9–10 mm. latum, lobis lateralibus latis, rotundatis vel obtuse angulatis, medioque multum angustiore obtuso saepius haud longiore praeditum, irregulariter variegatum ; calcar fere cylindricum, ovarium subaequans. Aliter ut in typo.

Tubers deeply palmate, with two or more elongate segments. *Stem* 10–20 (rarely –30) *cm. high. Leaves spreading and mostly arcuate-recurved, rather broadly lanceolate,* the upper distinctly dilated above the base, usually heavily spotted with brown. *Spike short and dense-flowered.* Flowers dark purple ; lip 7–8 mm. long, 9–10 mm. broad, with broad, rounded or bluntly angled side lobes, and a much narrower but obtuse central lobe generally not exceeding them in length, variegated with irregular darker lines and spots ; spur cylindrical, nearly as long as the ovary.

O. majalis, the ' *O. latifolia* ' of modern Continental authors, was founded by Reichenbach on a Saxon plant that flowers in May and June before any other Marsh Orchid. The original figure shows rather long, narrow, lanceolate foliage, which agrees well with a Dresden specimen in Herb. Mus. Brit. sent out by Reichenbach fil.

Reichenbach the elder issued a set of exsiccatae (no. 171) under the name of *O. majalis,* which differs from his plate and the Dresden example by its shorter and broader leaves, The majority of specimens in herbaria are more or less of this form. Haller's figure clearly depicts it, and it is the only form that I have seen in the lowland and subalpine marshes of Switzerland. From their description it would appear that Ascherson and Graebner intend such a plant for their race *pinguis* ; and as Barla in France, Schulze in Germany, and Vermeulen in Holland all figure a similar plant to represent ' *O. latifolia* ', it is probably the commonest form of the species. But it is likely that intermediates connect it with the narrow-leaved type.

The variety *occidentalis,* which I discovered last year (1933) in five different stations in Counties Clare and Galway, Ireland, differs from the typical species in its dwarfer habit, shorter, broader, and recurved leaves, and short dense spike of dark flowers, with a short central lobe to the lip. My specimens were collected between 16th and 20th May, at Ardrahan, Gort, Lough Bunny, and Poulsallagh, on the limestone, and at Lisdoonvarna, on the old red sandstone, in limited quantity in each locality and showing scarcely any appreciable variation. The new plant recalls *O. purpurella* by its short dense spike of deeply coloured flowers, but it is easily separable by its broader, recurved, and heavily spotted foliage, its clearly three-lobed labellum, and its longer cylindrical spur. And it also flowers a month earlier. As already remarked, however,

under *O. purpurella*, forms occur both in Ireland and the north of Scotland that seem to show intermediate features.

Col. Godfery describes in his ' Monograph ' (p. 219) a variety *eborensis* of ' *O. latifolia* ' (The Mystery Orchis), which may belong to *O. majalis*. It is well shown in his photographic plate H, f. 4. I met with a similar form, likewise in very small quantity, at Grassington, in Wharfedale, at the end of May 1920 ; and there is a good specimen in Herb. Mus. Brit. (Marshall no. 2305, Mallaranny, W. Mayo, 21. 6. 99, as *O. latifolia* v. *brevifolia* Reichb. f.) that is not very different. These plants are all very much dwarfer than var. *brevifolia*, as treated by Ascherson and Graebner, and require further observation before their real status can be determined. The varietal name ' *eborensis* ' is invalid owing to the omission of a Latin diagnosis.

7. *O.* ALPESTRIS, sp. nov.

O. latifolius race *impudicus* Asch. & Graebn. Syn. Mitteleur. Fl. iii, 736 (1907). *O. latifolius* subsp. *impudicus* Soó in Fedde, Rep. 30 (1927). *O. latifolia* var. *impudica* E. G. & A. Camus, Mon. Orchid. d'Europe, 234 (cum var. *Barlae* ?) (1928).

Icon. Barla, Icon. pl. 49, central figure, as *O. latifolia.*

Exsicc. Pugsley no. 517 (Zurs, Vorarlberg) (type) ; Reverchon, Lautaret, 1869, in Hb. Manchester, and Gap, 1871, in Hb. Kew., as *O. latifolia* ; Krättli, Bevers, 1868, in Herb. Mus. Brit., as *O. latifolia.*

Caulis 10–35 cm. altus, fistulosus. Folia erecto-patentia, plerumque supra medium latissima, inferiora subrotundo-obovata ad oblanceolata, omnia arcte vaginantia, valde et conspicue brunneo- vel purpureo-maculata. Spica laxiuscula, nonnunquam multiflora, bracteis quam floribus longioribus praedita. Flores magni, speciosi, saturate rubente-purpurei ; sepala lateralia raro maculata ; labellum 9–10 mm. longum, 10–12 mm. latum, planiusculum, subrotundo-obovatum, breviter 3-lobatum, lineis undulatis maculisque nigricantibus variegatum.

Tubers subpalmate with 2 (an semper ?) elongate ±spreading segments. *Stem 10–35 cm. high, fistular, with close leaf-sheaths,* and below 2–3 membranous sheaths, the uppermost of which usually develops a short, subrotund, reflexed leafy apex. *Leaves* 4 (rarely 5), *erect-spreading,* all except the uppermost obtuse and *broadest above the middle, the two lowest subrotund-obovate to oblanceolate,* the upper elliptic to lanceolate, *all heavily marked on the upper side with solid brown or purplish spots. Spike rather lax,* generally short, but *sometimes* long and *many-flowered ; bracts,* at least the lower, *exceeding the flowers,* lanceolate from a broad base, conspicuously nerved, ±suffused with dark purple. *Flowers large, showy, rich dark reddish purple ; lateral sepals* strongly reflexed, *rarely spotted : lip 9–10 mm. long, 10–12 mm. broad, nearly flat, subrotundobovate, shortly 3-lobed,* the lateral lobes broad and rounded, the central much smaller, cuneate, generally as long as the lateral but sometimes longer, the whole *variegated with blackish-purple waved lines and spots ;* spur conic⹁ cylindrical, often nearly as long as the ovary.

This beautiful orchid is intermediate between *O. majalis* and some forms of *O. cordigera* Fr. which inhabit eastern Europe. From the former of these it differs in its leaves, which are less numerous and, except the uppermost, always broadest above the middle and more obtuse. Its flowers are also larger, of a richer and darker purple, and with the lip, on an average, less trilobate. *O. bosniaca* Beck and Transsylvanian forms of *O. cordigera*, as represented in the exsiccata ' Fl. Austro-Hungarica Exsicc. no. 1851 ', bear a superficial resemblance to *O. alpestris*, but are separable by their more basal and often broader foliage, broader bracts, still larger flowers, and especially by their very short and broad conical spurs.

A new specific epithet has been applied to this plant, which seems essentially distinct from *O. majalis*, on account of the unsatisfactory nature of Crantz's *O. impudica* (Stirp. Austr. ed. 2, iv, 497 (1769)). Crantz's description contains only two distinctive characters, spreading segments of the tubers and an entire dentate labellum. It is doubtful whether *O. alpestris*, or indeed any other Marsh Orchid, exhibits a real taxonomic feature in the number and direction of its tuber-segments ; and an entire labellum might equally be said to be applicable to *O. latifolia* L. (*O. incarnata* auct. recent.). Linnaeus's character for *O. latifolia*, ' labium lateribus reflexum ' is stated by Crantz exactly to fit *O. impudica*, and this peculiarity does not point to *O. alpestris*. No habitat for his species is given by Crantz, albeit it must be presumed to be an Austrian plant ; and, in view of this and the vagueness of the description, his name seems best regarded as a ' nomen dubium '.

O. alpestris is evidently a widely spread species of the Alps of central Europe, where it grows, often in some abundance, in mountain swamps, generally at an altitude of 5–7000 ft., blooming in July and early August. It occurs in the Tyrol above St. Anton! in the Vorarlberg at and above Zurs! in Switzerland in the Engadine! at Andermatt! Murren! Zermatt! and Piora above Airolo! in Piedmont at Mont Cenis ; at Lautaret! and Gap in Dauphiny ; in the Alpes-Maritimes (Bafla) ; and in the eastern Pyrenees at Mont Louis! A specimen in Herb. Kew. from Nuremberg (Prechtelsbauer, Fl. Nürnberg, Dombach b. Fürth, 1883, as *O. latifolia*) has the aspect of a large and tall example of *O. alpestris*, with relatively small flowers such as might be expected in a lowland habitat.

In 1911 I collected two examples of *O. alpestris* × *maculata* in a locality near Mürren, where the parent species were growing in close proximity. In my experience *O. maculata* L. is not often seen near the habitats of *O. alpestris*.

II.

8. O. SAMBUCINA L.　Fl. Suec. ed. 2, 312 (1755) ; Sp. Pl. ed. 2, 1334 (1763); Mantissa alt. 486 (1771) ; Willd. Sp. Pl. ed. 4, iv, 30 (1805) ; Reichb. f. Icon. Fl. Germ. xiii, 64 (1851) et auct. recent.　*O. latifolia* var. δ L. Sp. Pl. ed. 1, 941 (1753).　*O. incarnata* Villars, Hist. Dauph. ii, 36 (1787) ; Haller, Icones Plantarum, 36 (1795).

O. (*Serapias*) *VII* Clusius, Stirp. Pannon. Hist. 239 (1583). *O. palmata sambuci odore* C. B. Pin. 86 (1623).   *O. palmata lutea, floris labio maculato* Seguier, Pl. Veron. Suppl. 249 (1754).   *O. radicibus palmatis, bracteis coloratis, labello circum-serrato trilobato, lobo medio emarginato* Haller, Hist. Helv. ii, 142 (1280) (1768).

Icones. Clusius, l.c. ; Svensk Bot. vi, t. 362 ; Fl. Dan. t. 1232 ; M. Schulze, Orchid. Deutschl. t. 22.

Plant generally 10–20 cm. high, with ±fistular stem and close leaf-sheaths. Leaves erect-spreading, narrowly obovate or oblanceolate, broadest above the middle, unspotted. Spike short, rather dense-flowered, with lower bracts exceeding the flowers. Flowers large, yellow or dull reddish purple with a yellow blotch on the lip ; lateral sepals reflexed, unspotted ; lip 8–10 mm. long, 9–11 mm. broad, flat, subrotund, obscurely trilobed, finely marked with purple ; spur large, conic-cylindrical, equalling or slightly exceeding the ovary.

β. *incarnata* Lamk. Encycl. Méth. iv, 597 (1798) ; Lois. Fl. Gallica, ii, 606 (1807) ; Lamk. & DC. Fl. Franç. iii, 251 (1815) ; Wahlb. Fl. Suec. i, 554 (1824) ; Sprengel, Syst. Veg. ed. 16, 687 (1826) ; Reichb. Icon. Botan. no. 1310 (1831). *O. incarnata* L. Fl. Suec. ed. 2, 312 (1755) ; Sp. Pl. ed. 2, 1334 (1763) ; Mantissa alt. 486 (1771), non ejusdem herb. ; Willd. Sp. Pl. ed. 4, iv, 30 (1805).

Icon. Reichb. l.c. f. 1095, as *O. sambucina* v. *O. incarnata* L. ; Fl. Dan. xvi, t. 2737, as *O. sambucina* f. *incarnata.*

Flowers flesh- or rose-coloured, with yellow blotch on the lip.

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EXPLANATION OF PLATE 31.

Orchis latifolia.   The specimen in the Linnean Herbarium.   (Natural size.)

INDEX.

[A star (*) denotes a name here published for the first time.]

Observations on the formation, development, and structure of the tuber of
Testudinaria elephantipes, and on the origin of the vegetative shoot.
By E. N. SPARSHOTT, M.Sc. (Communicated by the Botanical Secretary.)

(PLATE 32, and 4 text-figures)

[Read 15 March 1934]

INTRODUCTION

The investigations here described were carried out chiefly on young plants
of Testudinaria elephantipes grown from seed in the greenhouses of the George
Moore Botanical Laboratories, University College, Southampton. The seed
was collected in January 1927 by Professor E. L. Watkin, from plants growing
on the Southern Karroo, at a height of 3000 feet, where the vegetation receives
only rare and slight falls of rain.

As stated by Arber (1925) it is not unusual for a plant having such short and
irregular growing seasons to develop a storage tuber from which arise buds
capable of throwing up vegetative shoots and flowers during the few days
following rain. Testudinaria elephantipes is of this tuberous type, and the
development of its vegetative shoot, and no doubt of that of many related types,
depends more on the occurrence of rainfall than on the time of year. The
vegetative shoots of Testudinaria elephantipes, therefore, are not strictly annual,
since they die down at the end of each growing period and new ones are
developed after the next fall of rain.

THE ADULT PLANT

The tuber of Testudinaria elephantipes, like that of related species, e.g.
T. sylvatica, is subaerial. Its habit is shown in figs. 1 & 2. The semi-globular
tuber ultimately may attain a circumference of 3 metres and a height of 1 metre,
and may weigh several hundred pounds. The lateral surface of the tuber is
covered and protected by a thick hard cork layer, broken up into small regular
plates by deep fissures which appear and deepen as the girth of the tuber
increases. The cork thins off towards the base of the tuber, so that the lower
surface, which is irregularly flattened or concave, is covered only by a thin
brown skin. On this lower surface are the remains of old adventitious roots,
but recently formed roots are for the most part confined to the margin, as they
arise centrifugally. The roots form a fibrous and extensively branched
system, their diameter increasing somewhat as the tuber enlarges.

Each growing season a climbing vegetative shoot develops in the axil of
one of the scale leaves which surround the apex of the tuber (fig. 3, O, P).
This shoot dies down at the end of the growing season. Sometimes more than
one shoot arises in the axil of the scale leaf. As the plant gets older each new
vegetative shoot becomes longer and ultimately bears flowers. The plants
are dioecious and flowers are usually borne when they are about six years
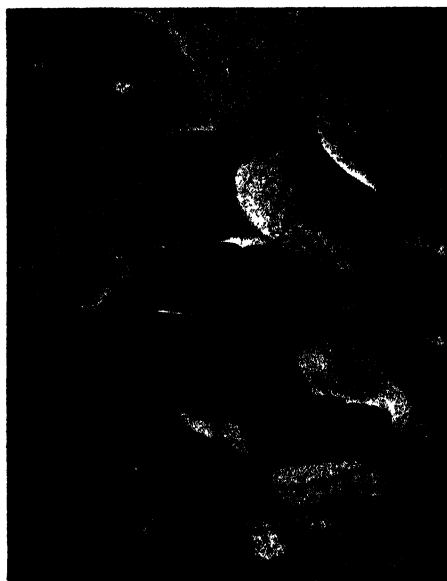
Fig. 1.—*Testudinaria elephantipes.* Three-year old tuber with vegetative shoot.
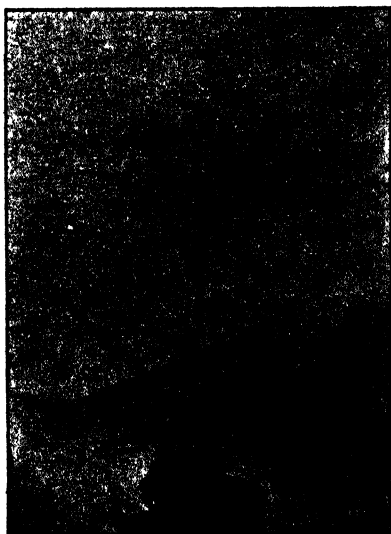
Fig. 2.—*Testudinaria elephantipes.* Five-year old tuber with vegetative shoot.

old. The remains of vegetative shoots commonly occur at distances from the apical bud varying with the age of the plant. This is due to the continuous horizontal growth of the tuber, whereby old shoot-bases, together with their subtending scale leaves, are carried further and further from the apical bud, and are finally lost in the corky mass of the tuber.

Each new vegetative shoot is at first thick and erect. In a few weeks the shoot elongates rapidly, twines, and becomes more woody. It develops scale leaves with wide sheathing bases at the first two or three nodes. Poorly developed leaves may appear at the nodes just above these scales. At still higher nodes true leaves are formed. The lowest internode is so short that the first node with its scale leaf is confluent with the tuber, and it is a bud in the axil of this scale leaf that gives the next season's vegetative shoot. The shoot system is therefore sympodial (cf. p. 608).

SUMMARY OF PREVIOUS WORK ON THE TUBER

The seedling development and the structure of the young and adult tuber of many members of the Dioscoreaceae have already been investigated, and *Tamus communis* in particular has received special attention. Although many authors have referred to the development of the seedling of *Testudinaria elephantipes*, all with the exception of Lubbock (1892) and Velenovsky (1907) have based their statements on analysis of and comparison with *Tamus communis* rather than on direct observations.

Dutrochet (1835) interpreted the young tuber of *Tamus communis* as the swelling of the first internode of the principal stem.

Von Mohl (1836) described in detail, but did not figure, the structure of the tuber of *Testudinaria elephantipes*. His seeds failed to germinate, and the youngest plants he had for study were three years old, while his main anatomical investigation was of an eight-year old tuber with a diameter of 3 inches. While admitting he could not verify his statements, he concluded that the development of the seedling and tuber of *Testudinaria elephantipes* was like that of *Tamus communis* of which he had abundant material. Like Dutrochet and later de Bary (1884) and Bucherer (1889) he considered the tuber to be the swollen first internode of the main stem.

Lubbock (1892) and Velenovsky (1907) both figured the seedling of *Testudinaria elephantipes* and considered the tuber to be a swollen hypocotyl. Velenovsky briefly described the development of the tuber. but made little reference to its internal structure.

Queva (1894) analysed the data in detail and reviewed the literature on Dioscorean tubers up to 1894. He described fully the development of the tubers of many of the Dioscoreaceae, especially that of *Tamus communis* and in less detail that of *Dioscorea sinuata*. These two species, at least during their early stages of development, undoubtedly most closely resemble *Testudinaria elephantipes*. Queva also had no seedling material of *Testudinaria elephantipes*, but assumed its development to be like that of the other two types. He concludes that the tubers are the result of a localised secondary

hypertrophy of the hypocotyl together with the first two internodes of the seedling axis.

1. *The Seed.*

Morphology. The seed of *Testudinaria elephantipes* is small, brown, and flattened, 4–5 mm. long and about 3 mm. wide. It is semi-circular, with a winged expansion developed from its curved side, which is remote from the embryo (fig. 3, A).

Anatomy. Within the testa is a small embryo situated at one end of, and embedded in, considerable endosperm. The testa consists of two layers of irregular cells with thick brown walls and is extended at one end into the thin fibrous wing.

The bulky endosperm contains abundant protein and fat, but no starch. Its thick cellulose walls are copiously pitted (fig. 3, Q). An embryo, carefully dissected from a seed which had been soaked in water for three to four hours and then kept in damp *Sphagnum* for a week, showed a very short hypocotyl and no suggestion of tuberisation.

Germination. Germination was successfully induced in two to three weeks, according to the age of the seed, by planting in pots of damp fibre and moss kept in a frame in a tropical greenhouse. As soon as the radicle appeared the pots were removed from the frame, but left in the hothouse until the first leaf had formed and tuberisation had become apparent. The seedlings were hardened off in a temperate house and then repotted in a mixture of peat-fibre and finely crushed brick.

During the development of the embryo the cotyledon expands, developing finally into a fan-shaped haustorium which penetrates the endosperm from end to end. Thus germination conforms to the more common type characteristic of Monocotyledons, in which part of the cotyledon forms a sucker and remains enclosed in the seed.

2. *Seedling development and tuber formation.*

The radicle emerges at the upper end of the straight edge of the seed, gradually pulling out the plumule, which is at first completely enclosed in a colourless scaly cotyledonary sheath (fig. 3, B). Within the sheath is a small undeveloped structure destined to become the first green leaf. This is covered by large multicellular hairs. This leaf when fully developed is larger than any leaf formed later on the vegetative shoots. Its emergence and further development are shown in fig. 3, C–H. It forms an assimilative organ while the seedling is still absorbing food from the endosperm. At this stage the radicle is frequently the only root developed, though occasionally there is also an adventitious root near by (fig. 3, F, G). A longitudinal section of such a seedling shows that the first leaf is given off practically at the same level as the cotyledon and immediately opposite to it. Transverse sections, however, also show the presence of a very short epicotyl (fig. 4, D–M). The plumular shoot at this stage thus consists of a stem apex, an almost negligible epicotyl, and one green leaf.

In nature the seedlings are exposed to strong sunlight, yet receive little water—conditions leading to restricted growth of the epicotyl and shoot system and to accumulation of assimilates. Food is passed from the seed to the short hypocotyl while that region is at the same time receiving assimilates from the leaf. Presumably food formation is in excess of consumption and the lack of space for its storage in the epicotyl has resulted in the tuberisation of the hypocotyl. That lack of opportunities for translocation may lead to tuberisation has also been suggested by Arber (1925) in *Zamioculcas Loddigesii*, an Aroid from Zanzibar.

It is two to three months before any further vegetative development occurs. Gradually less food reserves from the seed pass into the hypocotyl, while the assimilates from the leaf presumably increase to a maximum as the leaf expands. The lop-sided nature of the tuber at an early stage (fig. 3, E) is apparently due to the receipt of the bulk of the food reserves in the hypocotyl on the side next to the green leaf, resulting in greater tuberisation on this side, so that the radicle is gradually pushed into a lateral position.

No trace of fungal infection has been detected in any part of the plant.

A seedling four to six weeks old possesses a small sub-aerial tuber forming a round white body, partly enclosed in the cotyledon sheath and still attached to the seed (fig. 3, F). From the apex of the tuber arises the leaf with its long petiole and sheathing base. The seedling is held in the soil by the radicle and by such adventitious roots as are formed from the base of the tuber or near the radicle.

The rate of development of the seedling under greenhouse conditions appears to vary considerably according to the age of the seed and the time of year it is planted, so that it is impossible to say just when the leaves and roots may be expected to develop. A tuber may possess one leaf only for some time and yet develop an extensive root system. Often, however, a two months' old plant has developed a second leaf. This appears from within the sheathing base of the first leaf. It is often smaller than the first leaf, unless the latter has been damaged, in which case the second leaf develops more quickly and to a greater extent. The second leaf may show any stage of reduction, even to a small sheathing scale leaf.

The tuber gradually enlarges and becomes pale brown. A first leafy shoot was formed by some tubers less than three months old, when the tubers were no bigger than a large pea. In others the two green leaves were the only vegetative growths for four, five, or even six months, and the first leafy shoot did not appear until the tubers were the size of a small walnut. The shoot develops from between the sheathing bases of the first two green leaves, and when it first appears may be mistaken for a third leaf. After a time, however, a small swelling appears about the middle of its apparent petiole (fig. 3, J). This is the node from which the third leaf has arisen. Even when this leaf has fully developed, the terminal bud of the shoot and also the axillary bud of this leaf may be still enclosed in the sheathing base of the leaf. Occasionally two such nodes can be distinguished (fig. 3, K). The first leafy axis produced
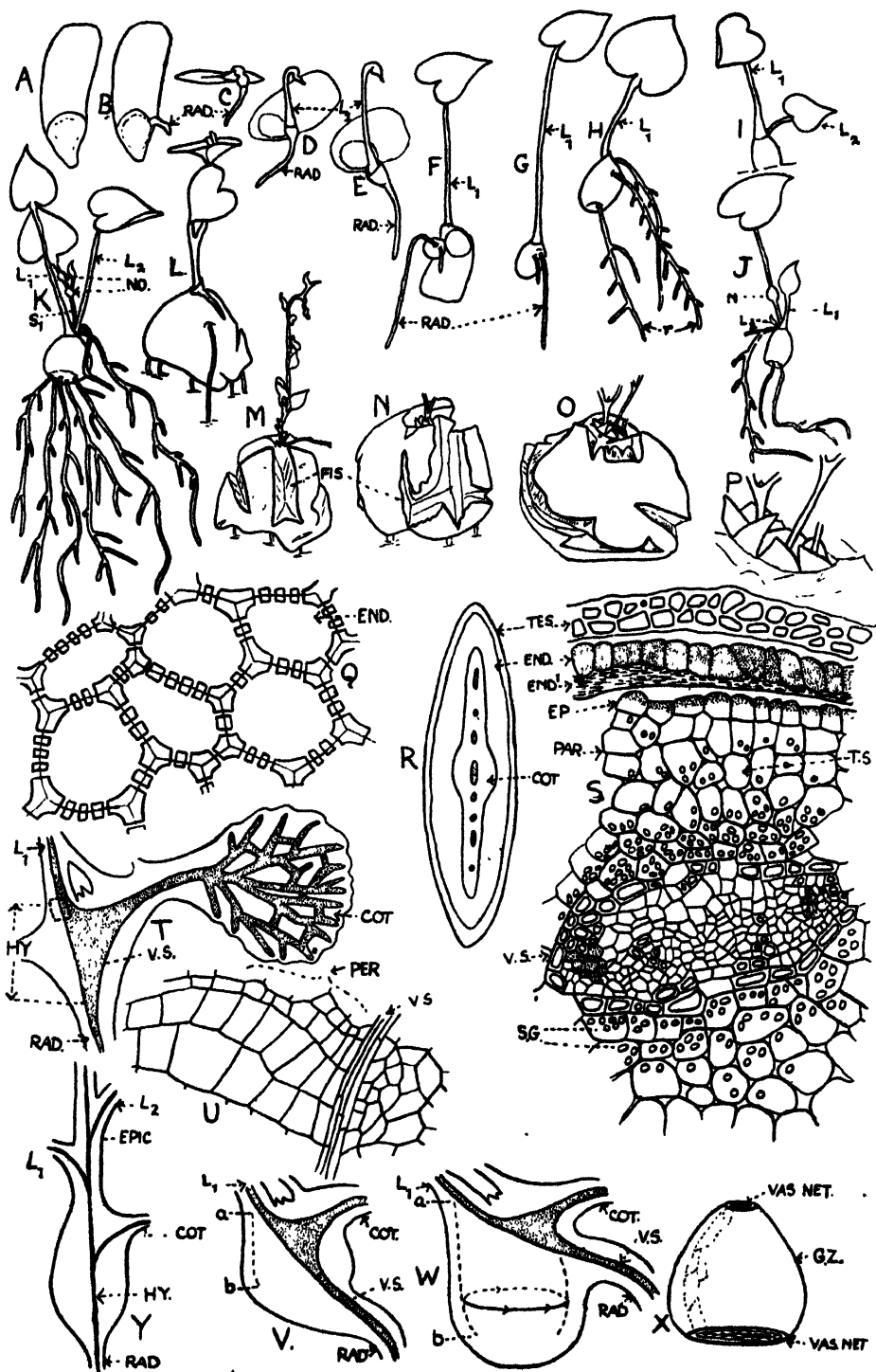
FIG. 3.

by the tuber rarely develops further than this. The tuber has by this time taken on its adult shape, i.e. semi-globular with a concave base. The radicle has developed into a much branched root system, which may persist for some time. Near it there is usually a small adventitious root, the second root to be formed. After the production of this second root others are rarely developed from the sides of the tuber, but are confined to its base, from any point of which they may appear at this stage (fig. 3, K). These give rise to the branching fibrous root system previously described. The tuber now has the appearance and consistency of a small potato flattened at one end ; it is covered by a thin continuous corky skin, and it very slowly enlarges.

The early development of the tuber markedly resembles Queva's description of *Tamus communis* and *Dioscorea sinuata* (1894). The tuber of *Tamus*, however, soon becomes elongated, and the leafy shoot does not appear until the second year. Queva's figures of *Dioscorea sinuata* bear a much closer resemblance to *Testudinaria elephantipes*.

The first appearance of fissures in the lateral surface of the tubers of *Testudinaria elephantipes* also varied considerably in the available material. The tubers were usually rather larger than a walnut and bore a second vegetative shoot before any crack appeared. In fig. 3, L–O, are shown tubers of different ages with fissures appearing, deepening, and extending.

<div align="center">EXPLANATION OF FIG. 3.</div>

RAD.=radicle.	*END.*=endosperm.
r=roots developed from base of tuber.	*END.'*=depleted endosperm.
	EP.=epithelium.
L_1 & L_2=first and second leaves respectively.	*S.G.*=starch grains.
	V.S.=vascular strand.
S_1=first leafy shoot.	*PAR.*=parenchyma.
NO.=node.	*PER.*=pericycle.
HY.=hypocotyl.	*a, b*=growth zone (position of origin).
COT.=cotyledon.	*G.Z.*=growth zone.
EPIC.=epicotyl.	*VAS.NET.*=vascular network.
TES.=testa.	*FIS.*=fissure.

A–O. Germination of seed, development of seedling, and early tuber formation. (For description, see text.)

Q. Walls of endosperm showing pits in section.

R. Diagram of a transverse section of a seed after germination showing cotyledon in section, embedded in endosperm.

S. Detail of portion of a transverse section of the seed after germination, with the endosperm almost depleted.

T, V, & W. Diagrams showing the development of the tuber with three successive positions of the radicle, during the emergence, the expansion, and the full development of the first leaf. Only a portion of the leaf stalk, the cotyledon stalk, and upper part of the radicle are shown in the figures. The vascular system is stippled.

U. Detail of part within dotted line in T.

X. Diagram showing the shape of the growth zone with apical and basal vascular networks.

Y. Diagram showing how the union of the vascular systems of root, hypocotyl, epicotyl, cotyledon, and green leaves would appear in longitudinal section if the internodes were not telescoped and the root not displaced.

3. *Anatomy of seedling and of young tuber.*

The anatomy of seedlings was investigated prior to and during tuberisation. Material was fixed in Flemming's weak solution and embedded in paraffin (M.P. 52° C.).

Seedlings in which the first leaf was still enclosed in the cotyledonary sheath (fig. 3, B), and seedlings in which the first leaf, though apparent, was pale green and not fully developed (fig. 3, C, D) were still attached to the seed. Some seeds were planted vertically, so that longitudinal sections parallel to the flat surface of the cotyledon could be made when the tuber was longitudinally cut.

The cotyledon consists of a mass of thin-walled parenchyma in which lies a much branched and anastomosing system of vascular strands (fig. 3, T). The strands, which may amount to sixteen or more at the edge of the cotyledon finally unite into a single strand. A transverse section through the centre of the seed shows that the cotyledon has a thickened midrib with tapering wings running through the endosperm (fig. 3, R). The cotyledon in this region has about eight vascular strands, consisting largely of parenchyma, in which are embedded a few annular and spiral tracheides, and phloem, composed of very narrow elongated cells with thin walls. The structure of the single strand in the cotyledon sheath is shown in fig. 3, S. The cells of the parenchyma immediately surrounding the strand are densely filled with large starch grains. The number of starch grains in each cell of successive layers diminishes rapidly towards the outside. The limiting layer of the cotyledon forms a well-defined epithelium, the slightly papillate cells of which bulge in the direction of the endosperm, giving the cotyledon an irregular outline. These cells have dense contents and their thin walls lie in contact with depleted endosperm cells, the walls of which remain and form a finely striated belt. Some cells of the cortex of the cotyledon form tannin sacs. A longitudinal section of the seedling possessing a small pale green leaf shows the vascular strand of the cotyledonary sheath cut longitudinally (fig. 3, T). This strand enters the hypocotyl and forms a vascular plate and links up with the root and leaf strands.

A longitudinal section of a seedling with its first leaf still enclosed in the cotyledonary sheath shows the short hypocotyl to consist, apart from the vascular strand, of small-celled parenchyma containing raphide sacs, but there is no suggestion of tuberisation. Many of the elements of the vascular strand are still in the procambial stage. In no case, however, do they appear multinucleate as described for *Tamus communis* by Arber (1925). In the tip of the undeveloped lamina of the first green leaf and in the apex of the radicle are a large number of raphide sacs.

The emergence of the leaf from a split in the cotyledonary sheath is accompanied by a slight but uniform thickening of the hypocotyl. This is brought about by the enlargement and occasional division of the parenchymatous cells. The upper part of this 'proto-tuber' is limited by an epidermis consisting of small cells slightly elongated tangentially, while the lower part is

surrounded by, and united to, the cotyledonary sheath, which is, at this stage, parenchymatous. Fig. 3, T, V, W, shows diagrammatically stages in the development of the proto-tuber with three successive positions of the radicle during the emergence, the expansion, and the full development of the first leaf.

The cortical cells at the base of the leaf traces where the latter join the hypocotyledonary vascular plate continue to enlarge, and may or may not become generally meristematic and divide in all directions to give rise to a mass of small-celled tissue. Ultimately the cells immediately outside the fused strands of the leaf and of the hypocotyl opposite the cotyledon become meristematic and divide regularly in a tangential plane (fig. 3, U). It is this layer of cells which is responsible for the formation of the meristem from which the bulk of the tuber is derived; the time of appearance of this tissue varies considerably. The initial irregular division of the cortical cells may continue for some time or the meristem may appear very early. Although there is no outer adjacent layer of cells showing the Casparian strip of an endodermis this meristem is considered to be of pericyclic origin, as it occurs immediately outside the vascular strand. It may be supplemented by some of the adjacent parenchyma, which may divide regularly and tangentially. The meristem ultimately consists of several layers of cells and accordingly is better termed a ' growth zone '. This meristematic activity is much greater towards the base of the hypocotyl, decreasing gradually and finally ceasing just above the point of union of the leaf traces with the hypocotyledonary trace, i.e. in the short epicotyl (fig. 3, V, ab). At the same time the growth zone gradually extends at both sides and passes round the tuber until it finally takes the form of an inverted cup with a hole in the bottom. This may take place by regular advance of the meristematic activity as indicated by the arrows in fig. 3, W, or at irregular intervals small meristematic zones may appear which ultimately unite. Owing to the point of origin of this meristem, and to its mode of development the root is carried round to the position shown in fig. 3, W, and the primary vascular tissue of the hypocotyl forms a plate beneath the apex of the tuber. Beneath it lies the cup-shaped growth zone (fig. 3, X) and the tissues formed by its activity. The meristem never covers either the apex or the base of the tuber, although both are supplied with tissue by its products. It gives rise to parenchyma towards the outside and to a small number of thin vascular strands and much parenchyma towards the inside.

Thus the tuber is formed by the hypertrophy and cell division of the parenchyma of the hypocotyl, but mainly developed by the activity of a meristem formed later in the pericycle of the hypocotyl and epicotyl. The meristem is ultimately responsible for the shape of the tuber.

As growth proceeds more of the tuber is exposed beyond the cotyledonary sheath. About the same time as the growth zone is developing, the tuber, which was at first covered by the white epidermis, turns brown owing to the formation of a thin layer of cork. The phellogen from which this is derived is of hypodermal origin. The cotyledon sheath also becomes suberised and forms
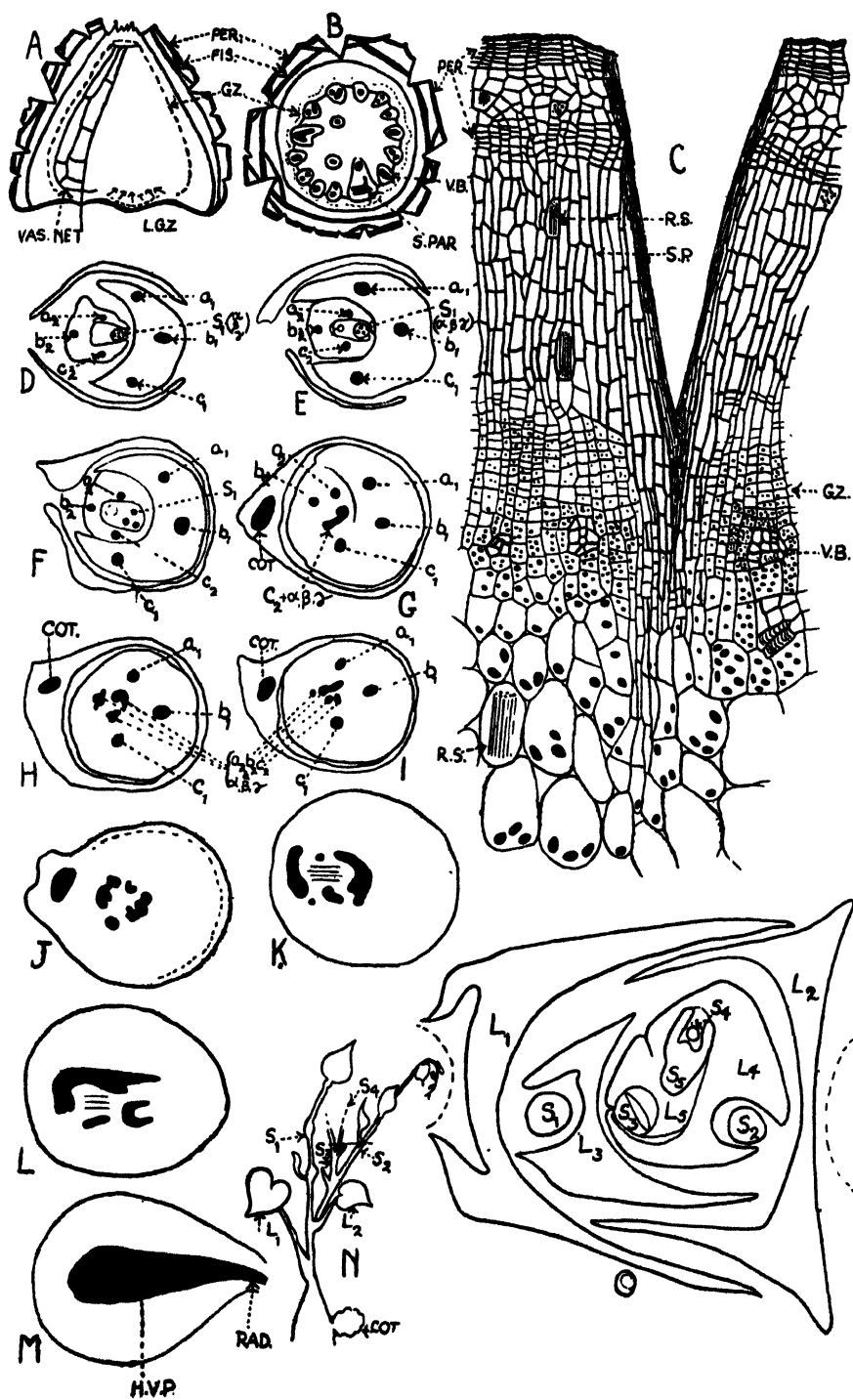
FIG. 4.

a further protective layer for the basal part of the tuber. The time of appearance of the phellogen varies to some extent with the conditions under which the plants are grown. Those grown under warm moist conditions retain their juvenile state much longer than those grown under dry conditions. Usually a three months' old tuber grown in a greenhouse has a thin corky covering (Pl. 32. fig. 1), which is continuous except at the apex, this being the point of origin of the vegetative shoots. In this region no cork is formed throughout the life-history of the tuber. A three months' old tuber contains samples of all the tissues found in adult tubers. A two-year old tuber has also all the external characteristics of a much older tuber, except for size and for the short vegetative shoots formed from it. A five-year old plant has all the adult characteristics, even to the long, twining, leafy shoots.

4. *Anatomy of three-year old tuber.*

The transverse diameter of the tuber examined was 1·7 in. and the greatest height was 1·5 in. (fig. 1). The convex surface was covered by a thick deeply fissured corky layer. The concave lower surface was irregular owing to the development of swellings. At the apex of the specimen was a healthy, short, but much-branched leafy axis. From the margin of the base sprang a number of young fleshy roots, others arose from the swellings on the base of the tuber, while elsewhere older fibrous roots persisted.

<div align="center">EXPLANATION OF FIG. 4.</div>

G.Z. = growth zone.	*S.PAR.* = parenchyma packed with starch.
L.G.Z. = local growth zone.	*S.P.* = suberised tissue.
V.B. = vascular bundle.	*PER.* = cork.
VAS.NET. = vascular network.	*R.S.* = raphide sac.

A. Median longitudinal section of a three-year old tuber. The position of the growth zone is indicated by dotted lines. The vascular network is shown in one half of the tuber. A local growth zone showing meristem (dotted) and direction of segments cut off by it (arrows) is seen on base of tuber.

B. Median transverse section of three-year old tuber.

C. Detail of part of a transverse section of the three-year old tuber showing fissure, growth zone, and its products. The walls which have become suberised as a result of fissure formation are shown by darker lines.

D–M. Diagrams of selected transverse sections from a series through a tuber possessing one well-developed leaf and a second young leaf.

> α, β, γ. = vascular strands of main axis (S_1).
> a_1, b_1, c_1 = vascular strands of first leaf (L_1).
> a_2, b_2, c_2 = vascular strands of second leaf (L_2).
> *COT.* = cotyledonary vascular strand.
> *H.V.P.* = hypocotyledonary vascular plate.
> *RAD.* = radicle strand.

N. Diagram showing the development of the main axis (S_1) and the subsequent vegetative shoot (S_2) and the position of the next two shoots (S_3 & S_4) as they would appear if the first internodes were not reduced.

O. A transverse section through the apex of a three-year old tuber showing the bud system; dotted lines indicate the position of old shoots now lost in corky crust of tuber. (See text.)

<div align="right">2 x 2</div>

(a) *The growth zone and its products.*

In a median longitudinal section the inverted cup-shaped growth zone is clearly distinguishable (fig. 4, A). Beneath the apex is a vascular network composed of the hypocotyledonary vascular plate now greatly augmented by secondary vascular tissue. To this plate all vegetative shoots are attached. Within the growth zone are a few thin secondary vascular strands running irregularly down the side of the tuber and anastomosing freely ; these are attached to the vascular network of the apex. In section they stand out as clear white patches, owing to the large number of starch grains contained in the parenchyma immediately surrounding the strands. The strands finally form a network over the base of the tuber, and it is from the points of union of these strands that all roots arise. The most recently developed roots were found on the same side of the tuber as the new shoots, and there is direct vascular communication between the roots and shoots of the current season. Von Mohl (1836) and Queva (1894) state that the vascular strands form more or less concentric rings corresponding to annual rings. They do not mention whether they really consider them to be comparable with the annual rings of a dicotyledon. The irregular course of the copiously branched and anastomosing vascular strands makes any tendency to concentric zoning difficult to detect. The arrangement was best determined by cutting the tuber longitudinally and examining the cut surface (fig. 4, A). This might be said to show three vascular rings, but, although these represent three periods of vegetative growth, they may or may not be annual rings. The growth zone and its derivative tissues are surrounded and compressed by a thick band of cork which is particularly thick around the apex. At the apex itself, where there is no resistant cork and no meristem, the tissues from the surrounding meristem tend to be pushed inwards along the line of least resistance. Thus the apex is supplied with tissue from the growth zone which surrounds it (Pl. 82. fig. 3). The displacement of tissues together with radial division in the cells of the growth zone results in a vertical elongation which approximates to the horizontal expansion of the tuber. The vascular net at the apex serves also a mechanical function in strengthening an otherwise weak position and preventing splitting in this region as a result of internal pressure.

Growth is more active in regions where vascular tissue is being differentiated than elsewhere. This results in the undulating outline of the growth zone (fig. 4, B) and the radial elongation of the medullary cells. Raphide sacs are abundant ; all other cells cut off towards the inside of the growth zone contain starch, especially those around the vascular tissue. The largest starch grains are found in the central medulla, which consists of large, very thin-walled parenchyma (fig. 4, C). The cells of the secondary parenchyma formed towards the outside of the growth zone become radially elongated and resemble those of the medullary rays. Raphide sacs are also found in this tissue and small leucoplasts are present in all other cells. A substance giving the inulin reactions was present in many of the cells,

Near the base of the tuber the growth zone curves slightly inwards and then disappears (fig. 4, A ; Pl. **32.** fig. 2).

The swellings noted on the base of the tuber examined are of common occurrence, and are the result of the activity of small meristematic zones formed in the parenchyma just beyond the basal vascular network. Regular rows of cells are cut off from these meristems, and the resulting growth resembles that of the main growth zone (fig. 4, A). Roots are developed on these swellings and disturb the otherwise concentric arrangement of the root system.

(b) *The cork crust.*

In a transverse section through the centre of the tuber the cork has an average thickness of 0·3 in. At this level therefore the cork forms about one-fifth of the thickness of the tuber. Fatty substances and tannin are abundant and a few raphide sacs are found in the cork crust. The cells are dead and many are filled with air.

Growth of the tuber proceeds slowly by the increase of the internal tissues. Thus a strain is set up in the originally smooth cork layer, and fissures which penetrate to the underlying parenchyma are formed. The parenchymatous cells surrounding the fissure become suberised, and a deeply seated band of cork, which links up with the first cork layer on either side of the fissure, is formed (fig. 4, B). If the number of fissures penetrating to the parenchyma is such that the parenchyma becoming suberised forms a continuous zone, then a new and complete band of cork is formed within this tissue and follows its outline. This sequence is repeated as new fissures develop and old ones deepen.

As stated by Von Mohl (1836) during the temporary exposure of the parenchyma following the formation of a fissure, small pale green chloroplasts appear immediately beneath the crack.

The first band of cork developed from the hypodermal phellogen is usually the thickest, consisting of about eight or nine rows of cells. Except for occasional irregularities brought about by the formation of radial walls in the phellogen (Pl. **32.** fig. 1) this cork formation is very similar to that characteristic of a Dicotyledon.

All primary tissue is soon lost in cork formation, and subsequent cork develops from the secondary parenchyma derived from the outer part of the growth zone. The cells which assume this meristematic activity develop irregularly and may in some places for a time constitute a double layer. A narrow band of cork may thus be formed simply by the formation of one or two tangential walls in these cells. This resembles the ' etagen ' cork described by Philipp (1923) for some Monocotyledons.

The appearance and duration of the phellogen seems to be determined by the appearance of fissures. If the fissures appear early the potential phellogen together with the surrounding parenchyma becomes suberised before it is actually established. There is therefore no fundamental difference between cork formation in this plant and that of a Dicotyledon.

The layers of cork stand out as narrow dark bands between the cells of the suberised parenchyma, because of the difference in the radial length of the cells. Walls of both cork cells and parenchyma are more or less equally suberised, though the parenchyma exposed after the first appearance of a fissure is often rather more heavily suberised. All these cells form more or less regular radial rows, since all have their origin in the cells of the growth zone (fig. 4, C).

A longitudinal section through the middle of the tuber shows that over its base the original cork layer persists, although the phellogen has become suberised. There are no fissures over this surface and so no further cork formation has occurred (fig. 4, A).

Old tubers frequently show two or more apical buds. In the examination of the three-year old tuber a possible explanation of this was found. The medullary ray cells are elongated radially and are doubtless under strain owing to the greater growth of the surrounding tissues (fig. 4, C). Fissures forming in the cork always abut on the medullary rays, for they are the regions of least resistant tissue. In one section examined a fissure was seen to have penetrated so deeply that it had actually penetrated the growth zone to a considerable depth and the meristem had obviously been endangered. The cells of the growth zone in this region and for some distance within it had been subjected to strain. At this point the growth zone had ceased to function, but on either side it appeared to have been stimulated into greater activity. Radial rows of cells had been pushed out tangentially by the growth and expansion of the tissue developed from the neighbouring portion of the growth zone. These secondary elements had expanded in the direction of least resistance, i.e. towards the fissure, and had subsequently met beneath it (fig. 4, C). Here, owing to the excessive divisions and growth of the meristem the cells had been forced together and had become partially suberised, and some had already become obliterated. Thus the region beneath the fissure had been strengthened.

As a result of this process there is a temporary collapse of meristematic activity at one point. If the damage caused by the fissure is not too great, gradually, as more and more cells are formed by the neighbouring meristem, the suberised region is carried outwards, until it comes to lie beyond the growth zone, and meristematic activity is once more established within it. If, however, the damage done by the crack is more severe it may possibly lead to the permanent collapse of the meristem in that area. A fissure penetrating the growth zone makes it impossible for the neighbouring meristem to repair the damage. The medullary parenchyma surrounding the fissure becomes suberised, but as it is beyond the growth zone it is not pushed out as the result of growth as in the previous case. A meristem of the nature of a phellogen may be established within the suberised area just as it is in the formation of the cork crust. This meristem is in direct contact with the inner tissues of the tuber, and from it adventitious shoots may arise. During the summer of 1933 tubers from which the apex with its entire bud system had been

removed, and halves of tubers taken longitudinally so that they contained no part of the apex, all developed adventitious shoots. The tissue bordering the wound became suberised and within this was cut out a phellogen which gave rise to cork cells towards the outside. An adventitious bud developed from the phellogen where this meets the growth zone, and its vascular tissue became linked up with that cut off by the growth zone during the current season.

5. *The origin and nature of the vegetative shoot.*

The first two green leaves developed by the tuber and all later-formed vegetative shoots are directly attached to the tuber and appear to develop directly from its substance.

The origin of the vegetative shoot in some members of the Dioscoreaceae has been investigated by earlier authors. Von Mohl (1836) considered the shoots of *Testudinaria elephantipes* to be borne adventitiously on the tuber. Bucherer (1889) concluded that the shoots of *Tamus communis* are axillary. Queva (1894) studied amongst others *Tamus communis* and *Dioscorea sinuata*, the species he considered most nearly related to *Testudinaria*. Though he had no young plants of *Testudinaria* he was led to suggest that the origin of the shoot of *Testudinaria* is similar to that of the other two types. He considered that although the internodes of the plumular axis are telescoped, the axis develops two nodes, from each of which a green leaf is produced in the first year. During the second year the buds in 'the axils of these leaves develop to give leafy shoots. The first internode of the shoot developed in the axil of the second leaf is totally reduced, so that its first node is confluent with the tuber. At this node a prophyll reduced to a small scale is developed, and in the axil of this scale leaf is a bud which is also directly on the tuber, and which will develop in the third period of vegetative growth. This bud develops to give a shoot of the third order, the first internode of which is again reduced and the prophyll likewise a scale. The bud in the axil of this scale is therefore on the surface of the tuber, and will develop to give a leafy stem of the fourth order and so on.

A similar explanation was given for the origin of the shoot of *Dioscorea sinuata*.

In order to determine whether such an explanation applies also to the origin of the shoots of *Testudinaria elephantipes*, series of transverse sections were made through tubers of various ages. The stages were as follows :—

1. Tubers with the first leaf well developed and a definite second small leaf.
2. Tubers with a leafy shoot developed.
3. Three-year old tubers which had developed several leafy shoots.

From the examination of these preparations it has been concluded that for the most part the vegetative shoots are of axillary origin, and that their development is similar in some respects to that described by Queva for *Tamus communis*. The possible adventitious origin of some shoots has already been discussed.

Testudinaria elephantipes may develop a short leafy shoot within the first three months. This shoot is the main axis, the first two nodes of which are formed early and bear the first and second leaves respectively, the internodes being reduced (p. 595).

An examination of fig. 4, D–M, representing successive transverse sections through a tuber possessing one well-developed leaf and a second young leaf, shows the general convergence of the vascular strands of the two leaves and of the cotyledon towards the main axis. Passing from the apex towards the base of the tuber, the three strands (a_2 b_2 c_2) supplying the second leaf fuse with the strands of the principal axis (α β γ) at the apex of the tuber, while the three strands of the first leaf (a_1 b_1 c_1) attach themselves to the axial strands at a lower level and within the tuber. At the level of fusion of the strands of the second leaf (a_2 b_2 c_2) with those of the main axis (α β γ), the base of the first leaf is partially fused with the main axis, though its strands (a_1 b_1 c_1) are free. Here the cross-sectional area is the same as that of the region above where the leaf bases are free. Any increase in cross-sectional area is practically negligible down to the first sign of fusion of the strands of the first leaf (a_1 b_1 c_1) with the combined strands of the main axis and the second leaf (fig. 2, G–I). Here the growth zone is definitely established and the cross-sectional area increases steadily down to the level of and beyond the hypocotyledonary vascular plate composed of the combined strands of the main axis, the two green leaves, and the cotyledon (fig. 4, M ; Pl. 32. figs. 4 & 5).

Fig. 3, Y, shows diagrammatically the union of the vascular system of root, hypocotyl, epicotyl, cotyledon, and green leaves as it would appear in longitudinal section if the internodes were not telescoped and the root not displaced.

It thus appears that the tuber is formed entirely from the hypocotyl and the lower part of the very short epicotyl, and that the internode above the epicotyl plays no part in tuber formation.

The bud system of older tubers is complicated by the double sheathing character of the prophyll with its unequal development on either side of its axillary bud, the very early establishment of a telescoped sympodium of many prophylls with their axillary buds and their 2/5 phyllotaxis.

Sections cut through the apex of two- and three-year old tubers (fig. 4, O) indicate the presence of shoots, greater in number than the years the tuber has lived, proving that the number of shoots developed does not necessarily coincide with the number of years of growth. Usually the position and origin of the outermost and oldest axes are difficult to trace, as the prophylls in the axils of which they were borne have become corky and are lost in the corky crust of the tuber. These bud systems, however, conform to the general plan described by Queva for *Tamus*. Thus the vegetative shoot S_1 in fig. 4, O, is borne in the axil of the prophyll L_1 and itself bears a prophyll L_2 which is confluent with the tuber owing to the telescoped nature of the first internode of the shoot. In the same way the shoot S_2 is in the axil of L_2 and the telescoped first internode of this shoot brings its prophyll L_3 on a level with the tuber, and so on. The apex is therefore a sympodium, and the bud or buds borne at

the lowest node in the axil of a scale leaf will give the vegetative shoots of the following season. This process is repeated. Fig. 4, N, shows diagrammatically the development of vegetative shoots as they would appear if the first internodes were not reduced.

SUMMARY.

The young plants used for these observations were grown from seed collected in the Southern Karroo.

The tuber of *Testudinaria elephantipes* is at first small, white, and spherical. Later it turns brown and develops a flattened or concave base and a thin continuous periderm.

In the older, massive, semi-globular condition the tuber has a thick, deeply fissured, corky crust. Towards the base of the tuber the cork forms a thinner layer, broken only by the protrusion of roots. Various developmental stages are figured.

There is no cork over a small area at the apex of the tuber. The growing point of the vegetative shoot is in this region, and is enclosed within a number of persistent scale leaves.

The seed contains a small embryo embedded in considerable endosperm. There is no suggestion of tuberisation in the embryo.

The development of the seedling is described and figured. A longitudinal section suggests that the plumular axis consists at first of little more than a stem apex and one leaf.

Lack of opportunity for translocation of food synthesised is probably the cause of tuberisation. An explanation of the lack of symmetry is suggested. Tuberisation is not due to fungal infection.

The anatomy of seedlings at different stages of development is described. The initial thickening of the hypocotyl results partly from cell division and partly from hypertrophy of the cortical parenchyma cells. Tuberisation is finally due to secondary growth originating in the pericycle.

The early development of the cork crust and the growth zone is described.

The structure of a three-year old tuber is dealt with in some detail. In general, the growth zone is hemispherical. Beneath the apex and just above the base no continuous meristem appears, though local growth zones may be found over the base. Vascular strands and medullary parenchyma are cut off towards the inside of the meristem, and secondary parenchyma towards the outside.

The vascular tissue forms a small flat network under the apex and a larger network over the base, and these plates are connected by a complex system of anastomosing vascular strands running down the side of the tuber towards the inside of the growth zone. These vascular systems form growth rings. The bulk of the tissue cut off from the growth zone is parenchymatous.

Fissures abutting on the medullary rays appear in the cork. The exposed parenchyma within the cork becomes suberised and a new band of cork is formed. Over the base of the tuber the original cork layer persists.

An explanation is given for the origin of adventitious shoots. .

The sympodial origin of the seasonal vegetative shoots formed at the apex of the tuber is described and figured.

The tuber is held to consist of a secondarily thickened hypocotyl and a very short epicotyl.

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EXPLANATION OF PLATE 32.

Fig. 1. Photomicrograph of a transverse section through a young tuber showing the first periderm (*PER*).

Fig. 2. Photomicrograph of a portion of the base of a three year old tuber in longitudinal section showing the disappearance of the growth zone (*G.Z.*) in that area. (Portion of the cork on the side of the tuber had been removed.)

Fig. 3. Photomicrograph of part of the apex as seen in longitudinal section. (*G.Z.* = growth zone, *V.B.* = vascular strands, *R.S.* = raphide sacs, *S.* = vegetative shoot.)

Figs. 4 & 5. Transverse sections taken through a young tuber (4) in the region of the hypocotyledonary vascular plate, and (5) below that region. (*G.Z.* = growth zone, *H.V.P.* = hypocotyledonary vascular plate, *V'B'.* = secondary vascular strands, *RAD.* = radicle vascular strand.)
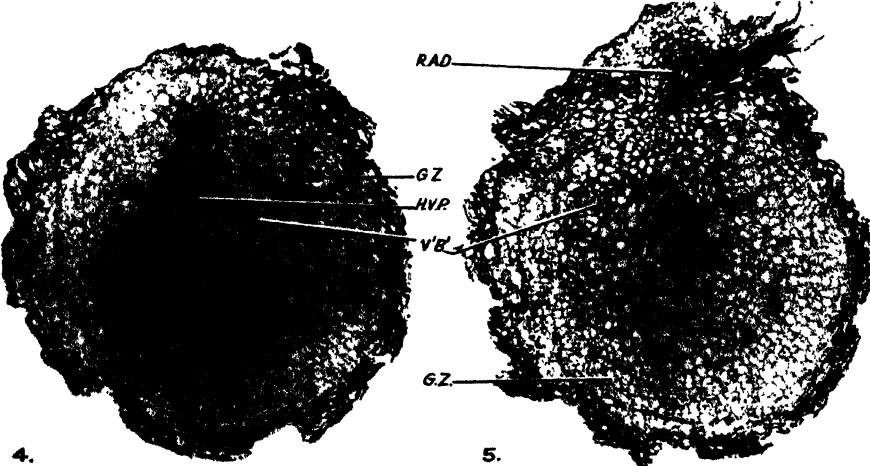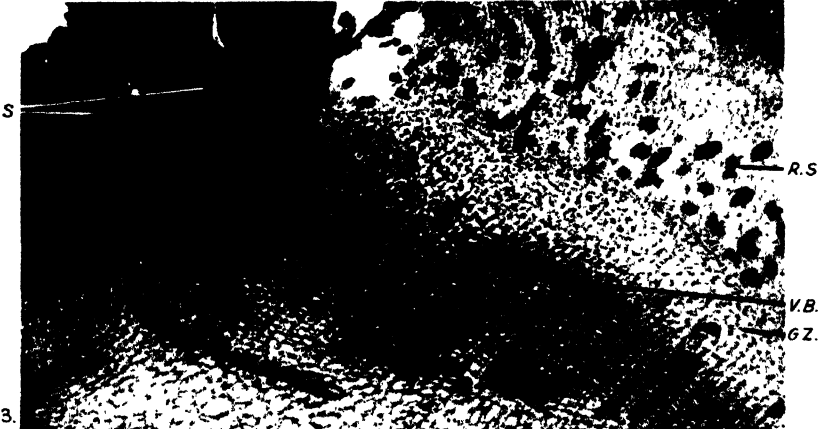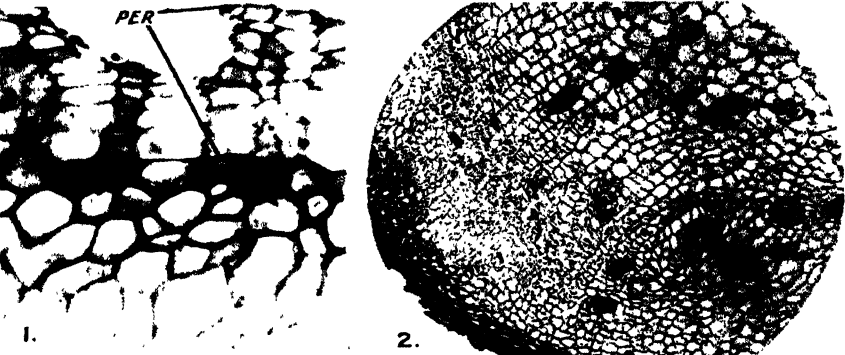
TUBER OF TESTUDINARIA ELEPHANTIPES.

The genera *Gaultheria* and *Pernettya* in New Zealand, Tasmania, and
Australia. By BRIAN L. BURTT and Sir ARTHUR W. HILL, K.C.M.G.,
M.A., Sc.D., D.Sc., F.R.S., F.L.S.

(With 8 text-figures and a map)

[Read 28 February 1929]

WHEN I paid my visit to the Dominion of New Zealand, at the invitation of the
New Zealand Government, in January and February 1928, I had the unique
experience of travelling throughout the Dominion with the late Dr. L. Cockayne.
In the course of our botanical tours the prevalence of natural hybrids among
so many of the New Zealand plants was brought very forcibly to one's notice,
thanks to Dr. Cockayne's able guidance.   In particular, when visiting Rainbow
Mountain, the remarkable series of hybrids between *Gaultheria oppositifolia*
and *G. antipoda* was quite astonishing.   These showed every gradation between
the two species, even to the extent of some of the calyx-segments of a flower
being fleshy, as in *G. antipoda*, while the others were dry as in *G. oppositifolia*,
a hybrid which up to that time had not been recognized by the New Zealand
botanists.

This discovery was naturally a stimulus to search for other *Gaultheria* hybrids
in the course of our tours, and later, at Waimarino, National Park, North
Island, interesting specimens of the bigeneric hybrid *G. depressa* × *Pernettya
macrostigma* were collected.   Thanks to Dr. Cockayne, Dr. Allan, Messrs. Scott
Thomson and Simpson, Miss Cranwell, and other collectors in New Zealand,
a remarkably rich series of hybrid Gaultherias has since been sent to Kew,
where they have been the subject of careful study by Mr. B. L. Burtt and
myself.

Examination of all the material of the genera *Gaultheria* and *Pernettya*
at Kew and at the British Museum was found to be necessary, in order to arrive
at an exact determination of the limits both of the two genera and of the
numerous species which have been described from time to time by various
authors, and also as to the extent and nature of hybridization.

Since there is a close relation between the Ericaceae of New Zealand and
Tasmania, it was also found necessary to examine critically the material of
these two genera in Tasmania, as well as the Gaultherias from the mainland
of Australia.

The following account is the result of our labours, which it is hoped may prove
to be of value to botanists in New Zealand and Australia, and help them to
settle some of the many puzzles with which they have been so long confronted
in these two genera, some of which can be solved only by experimental methods.

The specific epithet *perplexa*, which unfortunately has now to be discarded, was certainly well applied to the *Gaultheria* which we now consider to be a *Pernettya* !

With regard to *Gaultheria*, we are reinstating *G. Colensoi* as a good species, and maintaining both *G. depressa* and *G. antipoda* ; the former occurs also in Tasmania. A new species, *G. paniculata*, has been described. It has been found that the Gaultherias on the mainland of Australia differ from the Tasmanian ones, and a new species, *G. appressa*, has been described to include the mainland forms ; *G. hispida* being confined to Tasmania.

The genus *Pernettya* has been enlarged by the inclusion in it of ' *Gaultheria perplexa* ' from New Zealand, under its earliest name *Pernettya macrostigma*, and by the recognition that *G. lanceolata* of Tasmania belongs more properly to the genus *Pernettya*.

The account, therefore, deals with six species of *Gaultheria* from New Zealand, one being new, and three from Tasmania and Australia, one of them being a new species with a new variety. In the genus *Pernettya* there are two species in New Zealand and two in Tasmania.   ARTHUR W. HILL.

GAULTHERIA

Key to the Australian and New Zealand species of Gaultheria.

⊙ Flowers racemose.
  Calyx dry and unaltered in fruit. New Zealand.
    Leaves opposite or subopposite, ovate, cordate at the base, usually about 3·5 cm. long and 2 cm. broad ; flowers paniculate ; pedicels bibracteolate at the base, glabrous or minutely pubescent, about 5 mm. long ; corolla glabrous * ; anther-cells conspicuously biaristate .... 1. *oppositifolia*.
    Leaves alternate, narrowed, or at the most rounded at the base.
      Leaves oblong or elliptic-oblong, 3–5 cm. long and 1–2 cm. broad; branchlets setose ; flowers paniculate ; pedicels 4 mm. long, pubescent, and with some thicker hairs, bibracteolate at the base ; corolla glabrous ; anther-cells biaristate .... 2. *paniculata*.
      Leaves lanceolate, up to 3 cm. long and 1 cm. broad, or small, thick, c. 1·5 cm. long, elliptic to suborbicular.
        Branchlets setose and usually pubescent ; flowers racemose, often forming a panicle ; calyx segments with marginal outgrowths ; anther-cells biaristate .... 3. *rupestris*.
        Branchlets pubescent only ; leaves small, 1 cm. long and 0·5–0·8 cm. broad, oblong or suborbicular, veins impressed ; racemes terminal ; pedicels bibracteolate at the base ; corolla pubescent within .... 4. *Colensoi*.

Very occasionally pubescent within (see p. 614).

Calyx becoming enlarged and fleshy in fruit, more or
less enclosing the capsule. Australia and Tasmania.
Branchlets setose.
   Hairs on the branchlets spreading ; leaves averaging
     5·4 cm. long and 1·2 cm. broad; pedicels
     pubescent. Tasmania....................... 5. *hispida.*
   Hairs on the branchlets appressed ; leaves averaging
     4·9 cm. long and 1·6 cm. broad ; pedicels pubes-
     cent and with a few scattered, thicker hairs.
     Australian Mainland .... 6. *appressa.*
Branchlets glabrous, or with only an occasional setose
   hair .... 6. *appressa* var. *glabra.*

⊙ Flowers solitary, or occasionally subracemose towards the ends
  of the branches.

   Dwarf plant up to about 15 cm. high ; branchlets setose ;
    leaves elliptic to suborbicular, about 1 cm. long and
    0·5 cm. broad, crenate, often setose on the margins,
    veins impressed ; ' fruits ' large and fleshy, red or
    white .... 7. *depressa.*
   Erect plant up to about 2 m. high ; branchlets setose
    and sometimes also densely pubescent ; leaves
    variable in shape, thinner, and with sharper serrations
    than in *G. depressa* ; veins slightly prominent ;
    fruiting calyx fleshy, red or white, but much
    smaller than in *G. depressa* *, or sometimes dry .... 8. *antipoda.*

1. **Gaultheria oppositifolia** *Hook. fil.* Fl. N.Z. i, 162, t. 43 (1854) ; Handb.
N.Z. Fl. i, 175 (1864) ; Cheeseman, Man. N.Z. Fl. [ed. i], 407 (1906) ; Garden,
lxxxv, 412 (1911) ; Gardener's Chronicle, ser. 3, lii, 109 (1912) ; Cheeseman,
Ill. N.Z. Fl. ii, t. 123 (1914) ; Man. N.Z. Fl. ed. ii, 691 (1925).
   Brossaea oppositifolia (Hook. fil.) O. Kuntze, Rev. Gen. 388 (1891).
   Gaultheria multibracteolata Colenso in Trans. N.Z. Inst. xxiv, 389 (1892).

NEW ZEALAND. North Island :

Volcanic Plateau District :—Whakarewarewa, Nov. 1909, *Leland, Chase &
Tilden* 124. Kohutorua Creek, 8 miles north of Rotorua, Feb. 1872, *Kirk* 539.
Cliffs on shores of Lake Rotorua, Nov. 1928, *Allan* 5507 B, C. Near Lake
Rotorua, Jan. 1929, *Cockayne* 4275. Rainbow Mountain, near base, Feb. 1928,
A. W. Hill 10. Nov. 1928, *Allan* 5500, 5502, 5504 B. Rainbow Mountain,
Dec. 1928, *Barron.* c. 450 m., Jan. 1929, *Cockayne* 4263, 4266, 4271, 4273, 4274,
4280. Interior hilly country near Taupo, 1889, *H. Hill* (type of *G. multi-
bracteolata* Colenso). Tarawera, *Colenso* 348, 1018, 2362. Small hill between
Tarawera P.O. and foot of Turangakama Hill, Nov. 1928, *Allan* 5506 A, B, & Q.

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* Unfortunately only dried material is available for measuring, but in *G. antipoda* the
fleshy fruits seem to average about 0·4–0·5 cm. in diameter, in *G. depressa* about 0·7–1 cm.

Mangaone, Raetihi, near Ruapehu, 1933, *Attwood* K. 15. Headwaters of Wanganui River, draining from Mount Ruapehu, July 1933, *Attwood* K. 47, 54, 57.

Egmont–Wanganui District :—Mount Egmont, *Bidwill*. Mount Messenger, near the summit, April 1926, *Allan* 571 A. Nov. 1928, *Allan* 5505 D, E, F, G, & H.

An interesting point about this species is that it is the only member of the genus with opposite leaves. The consistency of this character is, however, somewhat doubtful. Some specimens, otherwise typical of the species, show a distinct tendency towards having alternate leaves, and it is scarcely possible to say from herbarium material whether this is natural in the species or due to hybridization with *G. antipoda*. On some seedlings raised in England the earlier leaves have been alternate, and later ones more or less opposite. This may be typical of the species, but, on the other hand, the parent plant may have been of hybrid origin strongly inclining to *G. oppositifolia*.

There are two specimens in the Kew collections collected at Whakarewarewa (*Cockayne* 725 and 4215), which appear on first sight to be typical *G. oppositifolia*. Dissection of the flowers, however, shows that in both the corolla is pubescent on the inside. This condition is also found in specimens of *G. antipoda*, but in other characters these plants are so close to *G. oppositifolia* that it does not seem possible that they can be hybrids between it and *G. antipoda*. Furthermore, as is noted under that species (p. 627), the corolla is not constantly hairy in *G. antipoda*, and the same applies in *G. rupestris*, the corollas of some specimens being quite glabrous on the inside, of others quite distinctly pubescent (p. 619). This character, we therefore conclude, is one which must not be over-emphasised.

This species has not been found on Mount Egmont since Bidwill collected it there, but Allan has recently collected it on Mount Messenger.

HYBRIDS :   .

  × *G. antipoda* Forst. fil. (p. 632).

  × *G. paniculata* B. L. Burtt et A. W. Hill (p. 634).

2. **Gaultheria paniculata** *B. L. Burtt et A. W. Hill* species nova, ob floribus paniculatis et corollis glabris *G. oppositifoliae* Hook. fil. maxime affinis, sed foliis alternis oblongo-ellipticis apice acute mucronatis basi angustatis, nec cordatis, inter alia facile distinguitur.

Frutex. Ramuli basi perulati, perulis inferioribus squamosis in folia gradatim transeuntibus, strigosi ; rami glabrescentes. *Folia* alterna, elliptica vel oblongo-elliptica, 3–5 cm. longa, 1–2 cm. lata, apice acute mucronata, basi in petiolum crassum 2 mm. longum subabrupte angustata, marginibus serratis, supra, pilis parvis in costa exceptis, glabra, conspicue reticulata, infra juniora sparse, in costa densiuscule, strigosa, vetustiora glabrescentia, basibus pilorum

FIG. 1.—*Gaultheria paniculata* B. L. Burtt & A. W. Hill.

A. Flowering branch (nat. size).   B. Flower (×6).   C. Corolla laid open and androecium (×4).   D. Calyx and gynaecium (×6).   E. Stamen (×16).   F. Part of infructescence (×2).   G. Persistent calyx and capsule (×6).

munita. *Inflorescentia* e racemis axillaribus apicem versus ramorum saepe ramosis paniculam terminalem formantibus composita. *Axis racemi* pilis albis brevissimis recte patentibus et, sparsissime, alteris crassioribus brunneis instructa. *Bracteae* carinatae, ovatae, acuminatae, circiter 3 mm. longae marginibus dentatis, dentibus brunneo-apiculatis. *Flores* pedicellati ; pedicelli 4 mm. longi, ut axis pubescentes sed pilis brunneis numerosioribus, basi bibracteolati, bracteolis 1·5 mm. longis bracteis similibus. *Calyx* 5-fidus (rarissime 6-fidus), tubo brevi circiter 0·5 mm. longo, segmentis triangulari-lanceolatis, 2–2·5 mm. longis, glabris. *Corollae tubus* cylindricus, 3·5 mm. longus, glaber, lobis 5 (rarissime 6) 1·2 mm. longis sub anthesin reflexis. *Stamina* 10 ; filamenta 1·5 mm. longa, dense papillosa, basin versus leviter dilatata, deinde iterum angustata. *Discus hypogynus* 10-lobatus, 4 mm. altus. *Ovarium* 5-loculatum, ovulis in loculis numerosis, glabrum, 1 mm. altum. *Stylus* glaber 2 mm. longus. *Fructus* capsularis calyce immutato suffultus.

NEW ZEALAND.   North Island :

Volcanic Plateau District :—Rainbow Mountain, Dec. 1928, *Barron.* Mangaone, Raetihi, near Ruapehu, 1933, *Attwood* K. 7, 16, 17, 22, 26, 30, 33, 34 Headwaters of Wanganui River, draining from Mount Ruapehu, July 1933, *Attwood* K. 46, 52, 53, 55.

Egmont–Wanganui District :—Near summit of Mount Messenger road, Nov. 1928, *Allan* 5505 A, B, C, D.

The affinity of this species is with *G. oppositifolia* and *G. rupestris*, and it agrees with both in having the calyx dry and not enlarged in fruit. Although Allan's specimens from Mount Messenger consist of young leaves only, there is little doubt that they belong to this species.

HYBRIDS :—

× *G. oppositifolia* Forst. fil. (p. 634).
× *G. antipoda* Hook. fil. (p. 635).

3. **Gaultheria rupestris** (*Linn. fil.*) *D. Don** in G. Don, Gen. Syst. iii, 841 (1834) ; A. Cunningham, Fl. Ins. Nov. Zel. Precurs. in Ann. Nat. Hist. ii, 49, n. 418 (1839) ; DC. Prodr. vii, 594 (1839) ; Hook. fil. Fl. N.Z. i, 161, t. 42 (1854) ; Handb. N.Z. Fl. i, 175 (1864), excl. vars. δ & ε ; Cheeseman, Man. N.Z. Fl. [ed. 1], 406 (1906), excl. syn. *G. Colensoi* Hook. fil. & *G. divergens* Colenso ; Illustr. N.Z. Fl. (Educ. Dept.), t. 37 (1909), as *G. perplexa* ; Cheeseman, Man. N.Z. Fl. ed. 2, 690 (1925), excl. syn. *G. divergens* Colenso ; Laing & Blackwell, Plants N.Z., ed. 3, 332, fig. 118 (1927).

Andromeda rupestris Linn. fil. Suppl. 237 (1781) ; Murray, Syst. Veg. 407, n. 16 (1784) ; Forst. fil. Prodr. 34, n. 195 (1786) ; Willd. Sp. Pl. ii, 1, 613 (1800) ;

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* R. Brown (2) has been generally quoted as the authority for this combination, but he only suggested that it should be made, and never actually made it himself.

R. Brown, Prodr. 559 (1810); A. Richard, Voyage de l'Astrolabe (Ess. Fl. N.Z.), 208, t. 27 (1832).

Brossaea rupestris (Linn. fil.) O. Kuntze, Rev. Gen. 388 (1891).

NEW ZEALAND. South Island:

Western District :—Omeroa Saddle, midway between Franz Josef and Fox glaciers, Nov. 1929, *Allan & Cockayne* 4312.

Fiord District :—Dusky Bay, *Forster* ; *Menzies*. Milford Sound, George Sound and Dusky Bay, 1862, *Hector* 43. Milford Sound, *Lyall*.

Var. α, **subcorymbosa** (*Colenso*) *B. L. Burtt et A. W. Hill*, comb. nov.
Gaultheria subcorymbosa Colenso in Trans. N.Z. Inst. xxii, 476 (1890).
Gaultheria glandulosa Colenso, l.c. xxviii, 600 (1896).
Gaultheria calycina Colenso, l.c. xxxi, 274 (1899).

NEW ZEALAND. North Island :

Ruahine–Cook District :—Hills on east of Wellington harbour, Dec. 1928, *Beddie* (4221, 4255, 4257 in herb. Cockayne). Wainui Hill, base of Rumutaka Range, April 1929, *Beddie* (4284, 4287, 4288 in herb. Cockayne). On eastern slopes of Ruahine mountain range, County of Waipawa, *H. Hill* (type of *G. subcorymbosa* Colenso). Ruahine mountain range, east side, *H. Hill* (type of *G. glandulosa* Colenso). Mt. Holdsworth, Tararua Mountains, Jan. 1906, *Cockayne* 9055. Near top of Ruahine Mountain range, 1847, *Colenso* 62. Mitre Peak, Tararua Mountains, c. 1000 m., Dec. 1925, *Allan* 569.

NEW ZEALAND. South Island : Aorere Valley, Nelson, Dec. 1861, *Travers* 1.

HYBRID :—

× *G. antipoda* Forst. fil. (p. 630).

Var. β, **parvifolia** *Hook. fil.* Fl. N.Z. i, 161, t. 42 (1854) ; Handb. N.Z. Fl. i, 175 (1864) ; Cheeseman, Man. N.Z. Fl. [ed. 1], 406 (1906) ; ed. 2, 690 (1925).

NEW ZEALAND. North Island :

Ruahine–Cook District :—Near summit of Ruahine range, a small shrub 2–3 ft. high on stony ridges, July–Sept. 1848, *Colenso* 1535.

NEW ZEALAND. South Island :

Sounds–Nelson District :—Nelson, *Bidwill* 60. Upper Wairau, 1850, *Monro* 91.

North-Eastern District :—Rocky ground near summit of spur of Mount Charon, Hanmer, Jan. 1919, *Wright* (4220 in herb. Cockayne).

Western District :—Mount Cook, near Hooker glacier, 710–1200 m., 1862, *Haast* 686. Kelly's Creek, Otira Valley, Jan. 1890, *Cockayne* 4200. Arthur's Pass, 1200–1500 m., Jan. 1925, *Oliver*. Arthur's Pass, 710 m., March 1929, *Cockayne* 4292. Mountains of Wilkins River, head of Lake Wanaka, *Butcher* (4313 in herb. Cockayne).

Eastern District :—Small shrub on hillsides in Alps, 600–1200 m., *Sinclair & Haast* 41. Along the source branches of the Kawai River, 600–1150 m., 1860–61, *Sinclair & Haast* 472. Sides of Mount Sinclair, 750–1350 m., 1860–61, *Sinclair & Haast* 111. Hillsides, Valley of Kawai and Eastern Hills, 1860–61, *Sinclair & Haast* 319. Cass, grassland at 540 m., *Foy* 562. Craigieburn Gorge, Waimakariri Basin, 690 m., Dec. 1890, *Cockayne* 4201. Mt. Peel, 2160 m., Jan. 1919, *Allan* 576. Slopes of Sugar Loaf Hill, Southern Alps of Canterbury, Nov. 1929, *Sledge* 450.

North Otago District :—Mt. Ida, Dec. 1908, *Aston* 561. Otago, Lake District, 750 m., *Hector & Buchanan*.

South Otago District :—High part of McCrae's run, Dec. 1853, *Munro* 33.

Fiord District :—Humboldt Mountains, Feb. 1929, *J. Scott Thomson & Simpson* (4258 in herb. Cockayne).
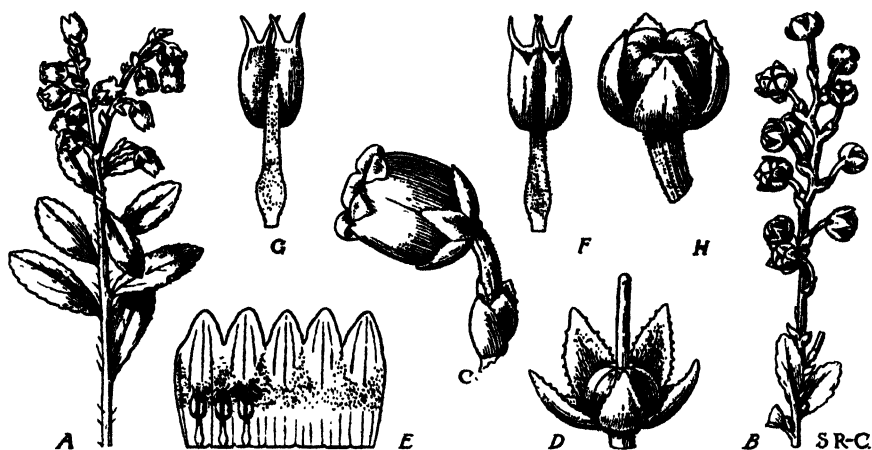
FIG. 2.—*Gaultheria rupestris* var. *parvifolia* Hook. fil.

A. Flowering shoot (nat. size). B. Fruiting shoot (nat. size). C. Flower (×4). D. Calyx and gynaecium (×6). E. Corolla laid open and part of androecium (×4). F. Stamen, front view (×12). G. Stamen, back view (×12). H. Persistent calyx and capsule (×6).

In this species the fruiting calyx is always dry. Hooker's statement—repeated by Cheeseman—'Calyx rarely baccate, but sometimes so ' is due to the fact that some of his specimens prove to be hybrids between *G. rupestris* and *G. antipoda*.

Hooker (8) described the small-leaved alpine variety under the name ' var. *parvifolia* ', and quoted the two specimens ' Nelson, on mountains, Bidwill ; Ruahine range, Colenso '. The latter is still the only specimen of this variety found in the North Island, which suggests that it may be only an ecological form. Hooker (10) arranged *G. rupestris* under five distinct varieties : his var. α, represented by Forster's plant from Dusky Bay, we regard

as the typical form, though the branchlets are setose instead of glabrous as he described ; var. β is the var. *parvifolia*, but here again the branchlets are often setose ; var. γ is not represented in the Kew Herbarium, but from the description * it probably differs very little from the type ; var. δ is *G. Colensoi* Hook. fil. of the ' Flora ', and is here reinstated as a species; while var. ε is certainly a hybrid between *G. rupestris* and *G. antipoda* as Hooker suggested (see p. 629).

Cheeseman, in both editions of his ' Manual ', arranged *G. rupestris* under two varieties ; ' var. *lanceolata*—leaves large oblong-lanceolate or obovate-lanceolate, acute, branches glabrous or more or less pubescent or setose ; var. *parvifolia*—leaves smaller and broader, oblong or oblong-ovate to orbicular-ovate, branches glabrous or rarely pubescent '. His first variety evidently included both the form found in the lowland western districts, South Island, and that found around Wellington and on the slopes of the Ruahine range.

In the present paper the type of the species is considered to be the lanceolate-leaved form with rather long racemes, which is confined to the western side of the South Island (Cheeseman's var. *lanceolata* in part). The form common on the slopes of the Ruahine range and around Wellington, as well as the specimen collected by Travers in the Nelson district, is referred to var. *subcorymbosa* (this variety was apparently included by Cheeseman in his var. *lanceolata*). The variety *subcorymbosa* has been described as a species on three separate occasions by Colenso ; his first epithet is the one now used. It is distinguished from the typical form by the leaves, which are oblong-lanceolate (in the specimens from near Wellington), or elliptic-lanceolate (in those from the Ruahine and Tararua Mountains), and by the corolla which is glabrous on the inside—a character which also serves to distinguish it from var. β *parvifolia*. The latter may usually be distinguished by the smaller thicker leaves (shortly oblong and seldom exceeding 2 cm. in length) ; Colenso 62 here referred to var. *subcorymbosa* is very close to Colenso 1535, the only Ruahine specimen of var. *parvifolia*, but the ease with which they may usually be separated warrants their retention until the species has been critically studied in its native habitats.

Some uncertainty exists as to the geographical range of *G. rupestris* in the North Island, since Cheeseman, who included both *G. Colensoi* Hook. fil. and *G. divergens* Colenso, says, ' not uncommon in hilly and mountainous districts from the Thames goldfields southwards, sea-level to 5000 ft.' On the evidence of the specimens examined, however, its distribution is definite and well marked. It is found in the neighbourhood of Wellington and northwards on the Tararua and Ruahine ranges, but nowhere else. Hybrids between *G. antipoda* and *G. paniculata*, of which *G. divergens* is probably one, show a certain resemblance to some forms of *G. rupestris*, and it may be that the identification of these as *G. rupestris* is the reason for the extended northward distribution given by Cheeseman and also for Kirk's (12) record of *G. rupestris* from Rotorua.

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* ' Leaves as in α, but more membranous. Branchlets pubescent and setose.'

The second variety, *parvifolia*, is common on the mountains of the South Island and, as mentioned above, has once been collected on the top of the Ruahine range.

HYBRIDS :—

×*G. antipoda* Forst. fil. (p. 631).
×*G. depressa* Hook. fil. (p. 631).
×*Pernettya macrostigma* Colenso (p. 642).
×*P. nana* Colenso (p. 644).

4. **Gaultheria Colensoi** *Hook. fil.* Fl. N.Z. i, 162 (1854).
Gaultheria rupestris var. δ Hook. fil. Handb. N.Z. Fl. i, 175 (1864).

NEW ZEALAND.   North Island :

Volcanic Plateau District :—Plains, base of Tongariro, June 1850, *Colenso* 2410.   Near Lake Rotoaira, Taupo, June 1850, *Colenso* 2376.   East side of
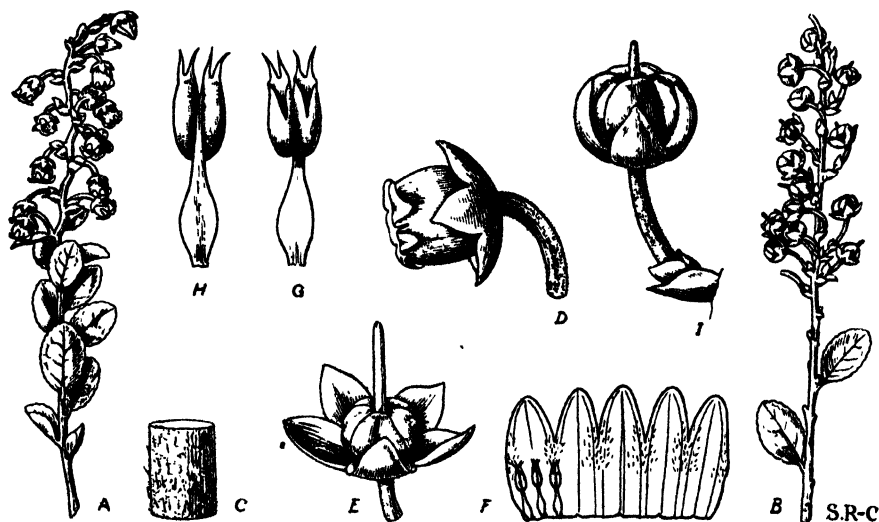
FIG. 3.—*Gaultheria Colensoi* Hook. fil.

A. Flowering shoot (nat. size).   B. Fruiting shoot (nat. size).   C. Part of shoot, to show indumentum (×6).   D. Flower (×4).   E. Calyx and gynaecium (×6).   F. Corolla, spread open (×4).   G. Stamen, front view (×12).   H. Stamen, back view (×12). I. Capsule and persistent calyx (×4).

the group of volcanoes, 1200–1500 m., Jan. 1908, *Cockayne* 4217.   Banks of Sulphur stream, west flanks of Ruapehu, Jan.–Feb. 1929, *Mrs. Martin* (4305 in Herb. Cockayne).   Mount Ruapehu, Jan. 1875, *Berggren* (in Herb. Upsal. et in Herb. Mus. Brit.).

This species closely resembles *G. rupestris* var. *parvifolia*. It may be distinguished by the pubescent branchlets, by the absence of bristles, by the

more orbicular leaves, and by the terminal racemes ; in *G. rupestris* they are axillary. The geographical distribution of *G. Colensoi* is a further indication that it is a distinct species. Hooker himself reduced it to a variety of *G. rupestris* in the ' Handbook ', and Cheeseman regarded it as a synonym of that species in the first edition of his ' Manual ' ; but it is not mentioned in the second edition. The leaf margins in some of the lower leaves are almost entire, while above they are crenately lobed. The leaves also tend to be rounded at the base and are broader at the base than at the apex. As in other species with racemose inflorescences the pedicels are bent down and the flowers are pendent, but as the fruits ripen the pedicels turn upwards so that the fruits are erect, as in the genus *Enkianthus*. (Fig. 3.)

HYBRIDS :—

    ×*G. antipoda* Forst. fil. (p. 632).

    ×*Pernettya macrostigma* Colenso (p. 643).

5. **Gaultheria hispida** *R. Brown*, Prodr. 559 (1810) ; Richard, Voyage de l'Astrolabe (Sertum Astrolabianum) 82 and t. 30 (1834) ; D. Don in G. Don, Gen. Syst. iii, 841 (1834) ; DC. Prodr. vii, 594 (1839) ; Hook. fil. Fl. Tasm. i, 241 (1857) ; Meredith, Bush Friends of Tasmania, t. 4 (1860) ; Bentham, Fl. Austr. iv, 141 (1864), pro parte ; Rodway, Tasman. Fl. 108 (1903).

TASMANIA. Without locality, 1933, *Lawrence* 303 ; *Milligan* 73. Western Mountains, May 1845, *Gunn* 305. Western Mountains, Dry's Bluff, North Spur, 1050 m., flowers and fruits white, 0·6–1·4 m., growing alongside *G. lanceolata*, *Giblin & Long* (584 in Herb. Tasm. Mus.). Arthur's Lakes, Jan. 1845, *Gunn* 305. Kangaroo Bottom, near Hobart, Aug. 1840, *Hooker*. North-east side Skiddaw (near Hobart ? *), 1905, *Caley* (in Herb. Mus. Brit.). Hobart Town, Jan. 1819, *Cunningham* 6. Mount Wellington, *Fraser* ; *Mrs. Tribe* ; 1842, *Gunn* 305 (in Herb. Kew & in Nat. Herb. N.S.W.). Mount Wellington *F. A. Rodway* ; *Maiden & Cambage* (in Nat. Herb. N.S.W.). Hartz Mountains, upper forest slopes, 600–900 m., *Gibbs* 6789. Huon Road, Nov. 1929, *Giblin*. Mount Arthur, *Mueller*. Banks of Derwent River, alpine region, Feb. 1904, *Brown* 2509. Macquarie Harbour, *Cunningham*. Mount Black, Rosebery, 440 m., Feb. 1930, *Nye* 7. Cradle Valley, 1050 m., gum forest association, Jan. 1925, *Weindorfer*. Hampshire Hills, in fruit, Feb. 1837, *Gunn* 305.

Gaultheria hispida was originally described by Robert Brown (2) from specimens which he collected in Tasmania, and later on specimens from the Mainland were included under his species. Careful examination of the various specimens from Tasmania, Victoria, and New South Wales shows certain constant differences between the Tasmanian specimens and those from the Mainland, which justify restricting Robert Brown's name *G. hispida* to the Tasmanian specimens.

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* In sailing from Sidney to England in Nov. 1805 Caley landed at Hobart and filled four boxes with plants.

Floral characters agree fairly closely in all the specimens, but there are marked differences in the leaf texture and shape, in the character of the hairs on the stems and leaves, and in the nature of the indumentum on the pedicels. It therefore seems desirable to treat the Mainland specimens as a distinct species ; it is also of interest to find that specimens from the northern limit of the area in New South Wales are practically glabrous, and are sufficiently distinct to be regarded as a variety.

In *G. hispida* from Tasmania the leaves are thicker and more coriaceous than in Mainland specimens, with all the veins deeply impressed on the upper surface. They are also narrower, relatively to their length, than those from Victoria and New South Wales ; usually from 5 cm. long and 1·2 cm. broad, though they may be as much as 2 cm. broad in one case, the length then being 8 cm., which is far larger than in any specimen from the Mainland. The average of ten specimens from Tasmania gives the ratio of leaf—length to breadth— as 5·4 cm.–1·2 cm., while a similar average for specimens from the Mainland is 4·9 cm. long, 1·6 broad. Again, the Tasmanian leaves are lanceolate or ovate-lanceolate, acute to acuminate, and gradually apiculate, while those of the Mainland specimens are elliptic-oblong or elliptic, and abruptly apiculate from an obtuse apex. The hairs on the two sets of specimens offer a striking contrast. In *G. hispida* from Tasmania the stems and midribs of the leaves bear spreading reddish bristles, while on the Mainland plants the bristles everywhere are closely adpressed. On the pedicels also there is a constant difference, for in the Tasmanian specimens they are covered with short, downy, whitish hairs, while in those from Victoria there are long, crisped, reddish hairs, as well as short downy ones. In the Mainland plants the adult leaves are more or less smooth above and the veins are scarcely—if at all—impressed (and then only the main ones), they are not hairy above except the midrib, which may be puberulous. The leaves of the Tasmanian plants are slightly hairy on the upper surface, and the midrib is pubescent on the upper surface.

A form showing certain differences from the type and found at a higher altitude is :—

TASMANIA : ' Trig.' Station, Dry's Bluff ; 1260 m. ; March 1929, Long (584 in Herb. Tasm. Mus.). 'About 1 ft. high ; fruit red in centre, rather more exposed than in type.'

This differs from the typical form in its dwarfer habit, narrower leaves (these are usually about 3 cm. long and about 0·5–0·2 cm. broad), and in the fruit which is half-exserted from the fleshy calyx.

6. **Gaultheria appressa** *A. W. Hill*, species nova, adhuc cum *G. hispida* R. Br. conjuncta, sed foliis minus coriaceis latioribus elliptico-oblongis vel ellipticis, floribus minoribus, pedicellis simul rufo-setosis et albo-pubescentibus differt.

Frutex ; ramuli petiolique pilis rufis arcte appressis densiuscule setosi. *Folia* elliptico-oblonga vel elliptica, circiter 5 cm. longa, 1·6 cm. lata, ex apice obtuso

abrupte apiculata, serrulata, tenuiter coriacea, supra nervo medio nonnunquam puberulo excepto glabra, subtus nervo medio pilis rufis appressis sparse setoso ; venae paullo impressae. *Flores* in racemis terminalibus dispositi ; pedicelli pilis minutis albis dense pubescentes et aliis majoribus rufis patule setosi. *Sepala* ovata, acuta, 2·8–3 mm. longa, 1·1–1·5 mm. lata, intus pubescentia (etiam marginibus). *Corolla* 4·5 mm. longa ; tubus intus hirsutus ; lobi 1·5 mm. longi, recurvi, obtusi. *Ovarium* et stylus glabra. *Fructus* capsularis calyce incrassato carnoso inclusus.—*G. hispida* Benth. Fl. Austral. iv, 141 (1869), partim.

VICTORIA : Bogong Ranges, *Mueller*. Big River under Mount Bogong, 1500 m., Jan. 1924, *Tadgell*. Cobboras Mountains, 900 m., Feb. 1854, *Mueller*. Macalister and Hardinger Ranges, 1868, *Mueller*. Gippsland, Mt. Mueller, 1500 m., *Luelmann & French* (in Herb. Nat. N.S.W.). Victoria Alps, under 1500 m., 1903, *Tadgell*. Towards Mount Feathertop, 1200–1500 m., *Tadgell*. Mount Donna Buang, Dec. 1927, *A. W. Hill*. Kyhean, east of Nimitybella, 1865, *Cambage*. Crewen State Forest, July 1917, *de Beuzeville*. Mount St. Bernard, Jan. 1900, *Maiden*.

NEW SOUTH WALES : Jenolan Caves, March 1900, *Blakely*. Barrington Tops, 1500 m., Dec. 1915, *Boorman*. Tumut District, April 1895, *Betche* (in Herb. Nat. N.S.W.).

Var. **glabra** *A. W. Hill*, var. nov., a *G. appressa* ramulis foliis et pedicellis glabris, foliis crassius coriaceis et angustioribus differt.—*G. hispida* R. Br. in Benth. Fl. Austral. iv, 141 (1869), partim ; Moore, Fl. N.S.Wales, 366 (1893).

NEW SOUTH WALES. Mountains head of Bellingen River (borders of New England), 1200 m., *Moore* (in Herb. Kew & in Herb. Mus. Brit.). Heads of Macleay and Bellingen River, *Moore* 139 (in Nat. Herb. Vict.). New England, *Moore* (in Herb. Nat. N.S.W.).

The New England Mountain specimen grows far removed from the localities where other Australian specimens have been collected. Moore's label on the sheet in the Melbourne herbarium reads 'A very pretty shrub growing among rocks frequently covered with snow—top of mountains.' The leaves are rather more leathery than those of specimens from Victoria and are also shorter and narrower and the veins are more impressed   An occasional hair can be found on the stems.

7. **Gaultheria depressa** *Hook. fil.* in Hook. Lond. Journ. Bot. vi, 267 (1847) ; Cheeseman, Man. N.Z. Fl. ed. 2, 689 (1925).
Gaultheria antipoda var. *depressa* Hook. fil. Fl. N.Z. i, 161 (1854) ; Fl. Tasman. i, 24, t. 73 (1857) ; Handb. N.Z. Fl. i, 174 (1864) ; Cheeseman, Man. N.Z. Fl. [ed. 1], 405 (1906).

Gaultheria antipoda Bentham, Flor. Austr. iv, 140 (1869) ; Rodway, Tasman. Flor. 108 (1903), non Forst. fil.

TASMANIA : Claybank, Ben Lomond, *Gunn* 516. Summit of Mt. Olympus, *Gunn* 516. Bain Bluff on pre-Cambrian schist, 1200 m., fruits scarlet, Feb. 1929, *Weindorfer* 5 (Tasm. Mus. Herb. 586).

NEW ZEALAND.   N. Island :

Egmont–Wanganui   District :—Mt. Egmont, Herb field, March 1916, *Cockayne* 2346 bis ;   Feb. 1928 *A. W. Hill* 7 ;   1,070–1,460 m., May 1929, *M. Thomson*, Eg. 7, 8, 9, 10, 11, 12.

Volcanic Plateau District :—Waimarino, near National Park Station, 3900 ft., Feb. 1928, *A. W. Hill* 3, 4, 5 (part), 6 (part).   Taupo country, Sept. 1847, *Colenso* 984.

Ruahine–Cook District :—Ruahine Mountain range, halfway up, July–Sept. 1848, *Colenso* 1570.

FIG. 4.—*Gaultheria depressa* Hook. fil.

A. Flowering shoot (nat. size).   B. Flower (× 4).   C. Fruiting shoot (nat. size).   D. Leafy shoot (nat. size).   E. Leaf (young, × 3).   F. Leaf (older, × 3).

NEW ZEALAND.   S. Island :

Without locality, Alpine, *Bidwill* ; *Lyall* ; *Travers*.

Sounds–Nelson District :—Nelson, *Bidwill* 58.

Eastern District :—Mt. Martius, 3–4,500 ft., March 1866, *Haast* 52.   Mingha Valley, Jan. 1928, *Oliver*.   Green Hill, Upper Poneter, trib. of R. Waimakariri, Jan. 1900, *Cockayne* 4206.   Mt. Bossa, Akaroa, *Laing* 567.   Sugar Loaf Hill, Cass, Nov. 1929, *Sledge* 451.   Cass, *Foy* 565.

Western District :—Arthur's Pass, 3,000 ft., Jan. 1928, *A. W. Hill* 1 ; March 1929, *Cockayne* 4293.

The type material of this species is that collected by Gunn on Ben Lomond, Tasmania. In preparing his 'Flora of New Zealand', Hooker found that specimens collected by Bidwill and Lyall on the Alps of the South Island, New Zealand, belonged to the same species. These, however, he regarded as an alpine variety of *G. antipoda* and he accordingly reduced his Tasmanian species to a variety of that species. It was not until the second edition of Cheeseman's 'Manual of the New Zealand Flora' was published that *G. depressa* was reinstated as a species ; a course for which there seems to be ample justification on account of its dwarf habit, smaller crenate leaves, and larger 'fruit'.

In *G. depressa* the leaves, especially when young, tend to be furnished with bristles on the leaf margins at the apices of the crenulations ; they are noticeably abundant in the Tasmanian specimens. The Tasmanian specimens also have the leaves rather more rounded than those from New Zealand.

All the specimens have the calyx much enlarged in the fruiting condition, the swollen calyx forming a deep cup in which the fruit is embedded. The free portions of the calyx in the ripe 'fruits' thus appear relatively short owing to the growth of the lower cup-like base of the calyx. The calyx in *G. depressa* is more fleshy and berry-like than in *G. antipoda*, and in addition to the habit etc. serves as a distinguishing character between the two species. The ripe fruits are described as being white, red or scarlet. (Fig. 4.)

HYBRIDS :—

   × *G. rupestris* var. *parvifolia* Hook. fil. (p. 631).
   × *Pernettya macrostigma* Colenso (p. 642).

8. Gaultheria antipoda *Forst. fil.* Prodr. 34, n. 196 (1786) ; Willd. Sp. Pl. ii, 1, 616 (1800) ; Pers. Syn. Plant. i, 482, n. 6 (1805) ; A. Richard, Voyage de l'Astrolabe (Ess. Fl. N.Z.), 211, t. 28 (1832) ; D. Don in G. Don, Gen. Syst. iii, 841 (1834) ; A. Cunningham, Fl. Ins. N.Z. Precurs. in Ann. Nat. Hist. ii, 49, n. 417 (1839) ; DC. Prodr. vii, 594 (1839) ; Hook. fil. Fl. N.Z. i, 161 (1854), Suppl. 333 (1855), excl. var. *depressa* ; Cheeseman ,Man. N.Z. Fl. [ed. 1], 405 (1906), excl. var. *depressa* ; ed. 2, 689 (1925) ; Laing & Blackwell, Plants N.Z. ed. 3, 332 (1927).

Gaultheria erecta Banks & Solander MSS. et Ic.

Gaultheria fluviatilis A. Cunningham, Fl. Ins. N.Z. Precurs. in Ann. Nat. Hist. ii, 49, n. 419 (1839) ; DC. Prodr. vii, 594 (1839).

Gaultheria epiphyta Colenso in Trans. N.Z. Inst. xxii, 474 (1890).

Brossaea antipoda (Forst. fil.) O. Kuntze, Rev. Gen. 388 (1891).

Gaultheria antipoda is the most puzzling of the New Zealand species of this genus, as Hooker and other early workers realised before the extent of natural hybridisation in the genus was appreciated. Now, although we know that some of their difficult specimens are hybrids, we still find ourselves confronted by problems which can be settled only by botanists working in New Zealand. We consider it best, therefore, to drop the use of varietal epithets and to arrange the specimens in three groups, mainly on their vegetative characters.

In the first place, however, it is desirable to give a sketch of the previous treatment of the species. In the ' Flora of New Zealand ' (i, 161) Hooker enumerated five varieties :—

Var. α. The typical form, represented by Forster's specimen in the Kew Herbarium.

Var. β, *fluviatilis*, based on *Gaultheria fluviatilis* A. Cunningham. A specimen from Keri Keri River, Bay of Islands, apparently represents the type of this species. Hooker included three specimens (Nos. 59, 61, and 62), collected by Bidwill at Nelson ; these, however, prove to be hybrids between *Pernettya macrostigma* and *Gaultheria antipoda*, or possibly *G. rupestris*.

Var. γ, *depressa*. This is based on *G. depressa* Hook. fil., which we regard as specifically distinct from *G. antipoda*.

' Var. δ, *microphylla* ; fruticulus prostratus, vage ramosus, foliis rigide coriaceis ovatis lineari-lanceolatisve 2–4 lin. longis, pedunculis pubescentibus glabratisve.'

This variety has been the cause of considerable confusion. There are three sheets at Kew written up by Hooker. One bears two specimens (*Colenso* 984 and 1570), each with ovate leaves, and both represent *G. depressa*. On a second sheet two specimens with linear-lanceolate leaves are mounted. These were collected by Colenso (985 and 2401) and both, we consider, are the hybrid *Pernettya macrostigma* × *Gaultheria depressa*. On the third sheet there are three specimens also with linear-lanceolate leaves : one labelled ' Herb. Sinclair ' and two collected by Dr. Lyall at Otago and Bluff Island, and all three represent *Pernettya macrostigma* Colenso.

' Var. ε, *ciliata* ; foliis parvis coriaceis lanceolatis serratis, dentibus setigeris.' No specimens exist at Kew or the British Museum, but it is probably very close to *G. depressa*.

Cheeseman recognized four varieties under *G. antipoda* in the first edition of his ' Manual ' (1906), which correspond to the first four of those given by Hooker. The first, to which Hooker had given no varietal epithet, he called var. *erecta* and added as a synonym *G. epiphyta* Colenso, published in 1890. Then follow the varieties *fluviatilis* and *depressa*, while to the variety *microphylla* he added *Pernettya macrostigma* Colenso as a synonym.

His next species was *G. perplexa* T. Kirk, with which he identified Hooker's fifth variety *ciliata*. *G. peplexa* and *Pernettya macrostigma* are undoubtedly synonymous, and with them agrees the third sheet of *G. antipoda* var. *microphylla* already mentioned. We consider they belong to the genus *Pernettya*, and the name *P. macrostigma* Colenso has priority (see p. 638).

In the second edition of the ' Manual ' the variety *depressa* was raised to specific rank and the var. *microphylla* was transferred to *G. depressa* as var. *microphylla* (Hook. fil.) Cheeseman.

The characters in which we have found marked variations are the following :—

(i) *Indumentum of the branchlets.* There are two distinct types : a short dense pubescence with a few scattered reddish setae, or a dense covering of appressed reddish setae with no, or only a minute, pubescence underneath. Intermediate types are uncommon.

(ii) *Presence of hairs on the inside of the corolla.* In Forster's specimen the interior of the corolla bears some short stiff hairs projecting horizontally inwards. These are also found in a few other specimens, but more commonly the corolla is glabrous. Since so many of the herbarium specimens are flowerless, it is impossible to ascertain the value of this character.

(iii) *Fleshiness of the fruiting calyx.* In *G. antipoda* the calyx normally becomes fleshy and red in fruit and grows up around the capsule as is usual in the genus. Some specimens, notably those collected by the senior author on Mount Egmont (Hill 8, 9), have the calyx green and dry. Others again (e.g. Allan 5507 A) show both dry and fleshy calyces on the same branch. The capsules which are subtended by dry calyces contain ripe seeds, apparently exactly similar to those from capsules surrounded by fleshy calyces, but whether they are equally viable (that is to say, whether the enlargement of the calyx may not be dependent upon fertilization), it has not been possible to test.

It may be noted here that no proof has been found of Hooker's statement (8) that ' in both *G. antipoda* and in *G. fluviatilis* capsular and berried fruit may be found on the same branch '. Both dry and fleshy calyces may be found, but the fruit itself is always capsular, although the capsule-walls may be coloured red. Hooker's statement may be due to the fact that hybrids between *Pernettya macrostigma* and *G. antipoda* were included with one of his varieties of *G. antipoda.*

(iv) *Leaf shape.* Generally speaking, the leaves of *G. antipoda* are fairly constant in shape, obovate or suborbicular, 1–1·5 cm. long and 0·8–1·3 cm. broad. One group, however, shows very marked variation from this general type. The specimens come from the district around the Bay of Islands, North Auckland. Amongst them is the type specimen of *G. fluviatilis* A. Cunningham, whose leaves average 1·25 cm. long and 0·4 cm. broad. This specimen, however, is only intermediate between the type and the extreme forms, some of which (e.g. Colenso, s.n.), have leaves averaging 1·25 cm. long, but only 0·2 cm. broad. It is noteworthy that the plants with narrow leaves frequently show hypertrophy in the flowering shoots ; many of the specimens from the north of the North Island are abnormal. Abnormalities of this kind have also been noticed in a collection just received from Mount Ruapehu and in some specimens dense bunches of small leaves are formed resembling those so common on English Willows ; this is possibly due to the attack of a mite.

G. antipoda presents difficulties to the taxonomist because of the apparent lack of correlation among the variations. Thus, dry calyces are found on gatherings (Hill 8, 9) from Mount Egmont, which have densely strigose branch-

lets, and also on Cockayne's 4213 from Whakarewarewa Heath, which has both pubescent and strigose hairs on the branchlets.

However, by using the characters of the indumentum of the branchlets and the leaf shape, which we believe to be of greater taxonomic value than variations in corolla and fruiting calyx, we have been able to divide the species into three groups. We do not propose to give these groups formal names, for their value is by no means certain, since the characters of calyx and corolla show variation within them.

GROUP A.   Plants with the white pubescence of the stem conspicuous and only a few strigose hairs.   Leaves generally obovate.

NEW ZEALAND.   Without locality, *Forster* ; *Colenso*.

NEW ZEALAND.   North Island :

North Auckland District :—Bay of Islands, 1826, *A. Cunningham.*   Whangarei, Aug. 1872, *Cheeseman* 85.

South Auckland District :—Tarura Creek, Thames, Nov. 1907, *Petrie* 564. Otorohanga, Nov. 1928, *Allan* 5507.

Volcanic Plateau District :—Whakarewarewa, Dec. 1905, *Cockayne* 4213 ; Nov. 1909, *Leland, Chase, & Tilden* 121.   Cliffs on shores of Lake Rotorua, Nov. 1928, *Allan* 5507 A.   Rainbow Mountain, near base, Feb. 1928, *Hill* 27. Rainbow Mountain, Nov. 1928, *Allan* 5503 ;   Dec. 1928, *Barron* ;   c. 450 m., Jan. 1929, *Cockayne* 4279.   Bank of Sulphur stream, west of Ruapehu, c. 900 m., Jan.–Feb. 1929, *Mrs. Martin* (4304 in herb. Cockayne).

East Cape District :—Small hill between Tarawera P.O. and foot of Tarangakuroa Hill, Nov. 1928, *Allan* 5506, I, O, X.   Wharerata Hill, Nov. 1928, *Allan* 5508.

Ruahine–Cook District :—Near Tangoro, Hawke's Bay, ' a bushy shrub 3 ft.', *Colenso* 3773.   Ruahine range, near summit, *Colenso* 1522.   Castle Point, July–Sept. 1848; *Colenso* 1911.   Woodville 1884, *Colenso*.   Hills east of Wellington Harbour, Dec. 1928, *Cockayne* 4256.   Wainui Hill, base of Rumutaka range, April 1929, *Beddie* (4285, 4286 in herb. Cockayne).

NEW ZEALAND.   South Island :

Sounds–Nelson District :—Nelson, *Travers*.   Nelson, 600 m., 1861, *Travers*. Kerr's Hill, Kikiwa, 600 m., Jan. 1929, *Allan* 550 B.

Eastern District :—Mount Grey Downs, Nov. 1896, *Cockayne* 4208.

GROUP B.   Plants with densely strigose branchlets and little or no pubescence.   Leaves generally more orbicular than in group A.

NEW ZEALAND.   North Island :

Egmont–Wanganui District :—Mount Egmont, small suberect shrub, calyx segments dry and green in ripe fruit, c. 900 m., Feb. 1928, *Hill*, 8, 9.   Mount Egmont, 945–1050 m., May 1929, *M. Thomson*, Eg. 1, 2, 3, 4, 5, 6.

Ruahine–Cook District :—Wood south of Dannevirke, *Colenso* (type of *G. epiphyta* Colenso).

NEW ZEALAND.   South Island :

Sounds–Nelson District :—Aorere, Nelson, Dec. 1864 and Jan. 1865, *Travers.*
Eastern District :—Mount Peel, c. 900 m., Jan. 1919, *Allan 575.*
Western District :—Arthur's Pass, 900 m., March 1929, *Cockayne* 4298.
North Otago District :—Cattle Flat, west of Lake Wanaka, Feb. 1893, *Petrie* (4210 in herb. Cockayne).
• South Otago District :—Otago, *Lyall.*   Flagstaff Hill, Dunedin, March 1929, *J. Scott Thomson & Simpson* (4294 A, B, C, D in herb. Cockayne).
Stewart District :—Stewart Island, *Cockayne* 2346.

GROUP C.   Plants of the *G. fluviatilis* type with narrow leaves.

NEW ZEALAND.   Without locality (probably Bay of Islands*), *Hooker, Colenso.*

NEW ZEALAND.   North Island :

North Auckland District :—Bay of Islands, *Sinclair.*   Shores of Bay of Islands, Sept.–Dec. 1826, *R. Cunningham* 417.   Keri Keri River, Bay of Islands, *R. Cunningham* 418.

HYBRIDS :

> × *G. oppositifolia* Hook. fil. (p. 632).
> × *G. Colensoi* Hook. fil. (p. 632).
> × *G. rupestris* var. *parvifolia* Hook. fil. (p. 631).
> × *G. rupestris* var. *subcorymbosa* (Colenso) B. L. Burtt & A. W. Hill (p. 630).
> × *G. paniculata* B. L. Burtt & A. W. Hill (p. 635).
> × *Pernettya macrostigma* Colenso (p. 641).

GAULTHERIA HYBRIDS

The first suggestion of the possible occurrence of natural hybrids among the New Zealand Gaultherias was made by Hooker (10) when describing his var. ε of *G. rupestris* (' ? A hybrid between *rupestris* and *antipoda* ').

The specimen in the Kew Herbarium has, as Hooker described, ' the habit and baccate calyx of *G. antipoda* ' and ' the racemose inflorescence of *G. rupestris* '.   From what we now know of hybrids among the Gaultherias and from an examination of his specimens he was quite correct in believing it to be the

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* Hooker spent three months in the Bay of Islands.   Colenso, in a list of his specimens sent to Sir William Hooker in 1841, writes ' 80. A species of *Gaultheria*; which, if not *G. fluviatilis* A. Cunn., is doubtless a new species.   Margins of streams, Bay of Islands.' This specimen may be the one referred to, as there is no specimen numbered Colenso 80 in the Kew collections.

hybrid *G. rupestris* × *G. antipoda* ; for not only do the stems bear the setose hairs typical of *G. antipoda* (also found on *G. rupestris*), and the leaves are broader and less acute than those of typical *G. rupestris*, but the majority of the fruits have fleshy calyx segments as in typical *G. antipoda*. One or two of the ripe fruits have dry calyces, while two fruits have one calyx segment dry and the other four fleshy, exactly as was noticed in the hybrid *G. oppositifolia* × *antipoda* on Rainbow Mountain.

Cheeseman makes no reference to this hybrid, but notes under *G. fagifolia* Hook. fil. : ' This appears to me to be a mere form of *G. rupestris* verging towards *G. oppositifolia*, or possibly a hybrid between the two plants.' This suggestion had previously been put forward by Kirk (12) and proves to be correct in so far as *G. fagifolia* is a hybrid, but the parents are *G. antipoda* and *G. oppositifolia*, between which it occupies an almost intermediate position.

In a recent paper, Cockayne & Allan (19) list six hybrids in *Gaultheria*. Two of these (277. *G. antipoda* × *perplexa*, and 279. *G. depressa* × *perplexa*) must now be regarded as bigeneric hybrids as we consider *G. perplexa* is a *Pernettya*, and its correct name is *P. macrostigma*. We fully agree with Cockayne and Allan as to three of the other four (276. *G. antipoda* × *oppositifolia* 278. *G. antipoda* × *rupestris*, 280. *G. depressa* × *rupestris*), which are well represented in the Kew Herbarium. As to the existence of the fourth (281. *G. oppositifolia* × *rupestris*), however, we are doubtful. We are inclined to think that the records of it are probably due to confusion with *G. paniculata* and with the hybrid *G. paniculata* × *antipoda*.

Gaultheria rupestris × G. antipoda

Hybrids between the various forms of these two species frequently occur, and may be conveniently tabulated as follows :—

(1) *G. rupestris* var. *subcorymbosa* × *G. antipoda*.

NEW ZEALAND.   North Island :

Ruahine–Cook District :—Hills east of Wellington Harbour, Dec. 1928, *Beddie* (4223 A, B, C, & D, 4224 in Herb. Cockayne).   Wainui Hill, April 1929, *Beddie* (4289, 4290, 4291 in Herb. Cockayne).

These were found growing near both the parents.   The specimens from the Wellington Hills are all more or less intermediate in character, with the leaves broader in proportion to their length than in pure *G. rupestris* ; the flowers may be in short racemes or sometimes they may be either solitary or in short racemes on the same plant.

No. 4289 from Wainui Hill, with its fleshy fruiting calyx, is much nearer to *G. antipoda* in that respect, but its flowers are in short racemes and the leaves are intermediate in character.   Nos. 4290 and 4291 are similar, but the mature calyx segments are scarcely or only slightly fleshy and do not enclose the capsule.

(2) *G. rupestris* var. *parvifolia* × *G. antipoda.*

NEW ZEALAND.   South Island :

Western District :—Omeroa Saddle, (?) 450 m., *Allan & Cockayne* (4306, 4307, 4308, 4309, 4310, 4311 in Herb. Cockayne).

Of these No. 4306 is almost typical *rupestris* var. *parvifolia*, except for the hairy stems and intermediate type of leaf.   The remainder have broader rounded leaves, more typical of *G. antipoda*, densely strigose stems, and the racemes, except in 4311, are shorter than in *G. rupestris*.   Cockayne has labelled all these ' *G. antipoda* × *rupestris* (Westland lowland jordanon) ', which is the typical form of *G. rupestris*, but *G. rupestris* var. *parvifolia* seems the more probable parent.

The lanceolate character of the leaves is not noticeable in these hybrids, but rather, except for Nos. 4306 and 4311, the leaves are almost orbicular in outline.   Unfortunately none of these specimens is in the fruiting stage.

The three following specimens, Aorere Valley, Nelson, 540 m., Dec. 1861, Travers 6 ; Punch Bowl Creek, Arthur's Pass, Dec. 1929, Sledge 505, 506, as well as Hooker's original *G. rupestris* var. ε, are a little difficult to place. From the leaf shape and the racemose inflorescences, typical *G. rupestris* or *G. rupestris* var. *subcorymbosa* may be one parent, as this variety has been recorded from Nelson.   The general facies indicates that they are undoubtedly hybrid in origin, but the Nelson plant and Sledge's 505 are more lax in habit than any of the other hybrids between *G. rupestris* and *G. antipoda*.   Sledge 505 has a single ripe fruit, and this shows the characteristic swollen calyx of *G. antipoda.*

Gaultheria rupestris var. parvifolia × G. depressa

NEW ZEALAND.   South Island :

North Otago District (?) :—Lake District, 1864–65, *Hector & Buchanan* 14, pro parte.

South Otago District :—Flagstaff Hill, Dunedin, March 1929, *J. Scott Thomson & Simpson* (4295 A–L in Herb. Cockayne).

The most interesting *rupestris* hybrids are those with *G. depressa* collected by Messrs. Scott Thomson and Simpson on Flagstaff Hill, Dunedin.   The specimens come from twelve different plants and are all very similar.

The plants are dwarf shrubs 10–15 cm. high, the stems bear setose hairs and the leaves, about 1 cm. long and 6 mm. broad and sometimes bristly-ciliate, are intermediate in type between those of the parents.   The inflorescences are short few-flowered racemes (corolla—only one withered example found— with a few hairs on the inside).   The fruits are of particular interest since in some the calyx segments are wholly fleshy, in others the base may be fleshy and the tips or upper half dry, while in a few flowers one or two segments are fleshy and the others are quite unswollen.   The false fruit even when most fleshy is smaller than in *G. depressa.*

Gaultheria Colensoi × G. antipoda

NEW ZEALAND.   North Island :

Volcanic Plateau District :—Near Rotoaira, Taupo, Sept. 1847, *Colenso* 986.

The sheet which Hooker wrote up as *G. Colensoi* bears three specimens, all of which were collected by Colenso.   Of these, two agree with one another and with Hooker's description of *G. Colensoi*.   The third, however, has bristly branchlets, much thinner leaves with sharper serrations and solitary or sub-solitary flowers which have the calyx slightly fleshy in fruit.   All these characters point to its being a hybrid with *G. antipoda*.

Gaultheria oppositifolia × G. antipoda

NEW ZEALAND.   North Island :

Volcanic Plateau District :—Whakarewarewa Heath, Dec. 1905, *Cockayne* 4214.   Cliffs on shores of Lake Rotorua, Nov. 1928, *Allan* 5507 D, E, F, G, H, & I.   Rainbow Mountain, near base, Feb. 1928, *A. W. Hill* 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26.   Rainbow Mountain, near base, Nov. 1928, *Allan* 5501, 5504 A.   Rainbow Mountain, Dec. 1928, *Barron*.   Rainbow Mountain, c. 450 m., Jan. 1929, *Cockayne* 4259, 4260, 4261, 4262, 4264, 4265, 4267, 4268, 4269, 4270, 4272, 4276, 4277, 4278, 4281, 4282, 4283.   Near Motu-kino village, 10 miles east of Lake Taupo, June 1850, *Colenso* 2368.   Motukino, near Lake Taupo, Feb. 1872, *Kirk* 520.   Near Lake Tarawera, *Kirk*.

East Cape District :—Small hill between Tarawera P.O. and foot of Turanga-kama Hill, Nov. 1928, *Allan* 5506 C, D, E, F, G, H, J, K, L, N, P, R, S, T, U, V, W, & Y.

In *Gaultheria oppositifolia* the leaves are broadly ovate to ovate-lanceolate, and cordate at the base.   Strigose hairs occur on the midrib and veins on the back of the leaves, which, typically, are opposite.   Occasionally, however, some of the leaves may not be quite opposite in specimens which are otherwise typical.   The stems are typically glabrous, but in one or two specimens a few strigose hairs may be found.   The inflorescences are terminal panicles and neither the calyx segments nor the fruits become fleshy as the fruit ripens. It may be that the plants with a few hairs on the stems and those in which the leaves are not always opposite are of hybrid origin with *G. antipoda*, crossed back possibly more than once with *G. oppositifolia*, and showing only a mere trace of the *antipoda* parentage.

In *G. antipoda*, on the other hand, the more leathery rounded or orbicular-ovate leaves are scattered, the stems are beset with strigose hairs and the flowers are borne singly in the leaf axils.   Further, the calyx segments become fleshy as the fruit ripens and enclose the fruit, the wall of which may become coloured like the calyx segments.

G. oppositifolia and *G. antipoda* grow together in several places, and wherever they do so a remarkable series of hybrids occurs showing every gradation from one to the other species.

The first indication of hybridity is shown when plants are found growing

in an *oppositifolia* colony with hairy stems and with leaves becoming alternate, but in these forms, which closely resemble *oppositifolia*, the inflorescences remain terminal, though the panicle is less definite and has fewer and laxer branches than in the dominant parent ; the calyces, however, remain unswollen. As the influence of *G. antipoda* becomes more pronounced, the leaves become smaller and thicker, and also more polished and leathery, with an undulate or crenulate margin, the foxy-red strigose hairs on the stems become more pronounced, and the inflorescences are in the form of short axillary racemes— sometimes single, at other times branched—situated in the axils of the terminal leaves of a shoot. The most interesting indication of the hybrid nature of some of these forms, which have long puzzled the systematist, was the dis- covery of plants, growing on Rainbow Mountain in the North Island, with ripening fruits in which one, two, or three of the calyx segments were fleshy, the others of the same flower being dry, while sometimes all the calyx segments of one fruit were found to be fleshy, yet in another fruit all were dry. The plants showing these interesting characters resembled *G. oppositi- folia* generally, but with more spreading branches and with the leaves like those of *oppositifolia*, but smaller and alternate ; the stems were strigosely hairy, the inflorescences were axillary or subterminal simple or branched racemes.

In the year 1850, Colenso collected a shrubby *Gaultheria* 4–5 ft. high, ne Motukino, 10 miles east of Lake Taupo, to which he gave the manuscript name *G. intermedia* (no. 2368), and Kirk, collecting at the same place in 1872, found a similar plant and records ' only four or five specimens observed after the closest search '. The two specimens were subsequently described by Hooker (8) under the name *G. fagifolia*, and Colenso's plant is cited as the type specimen ' of this most distinct species '. *G. fagifolia*, however, proves to be about the midway form in the great swarm of hybrids between *G. oppositi- folia* and *G. antipoda*, and can be connected with either species by a series o intermediate forms.

One of the most interesting localities for studying the hybrid population resulting from the crossing of *G. oppositifolia* and *G. antipoda* is at about 1500 ft, on Rainbow Mountain, near Rotorua, Volcanic Plateau District, N. Island, which the senior author visited with Dr. Cockayne in February 1928 and where a series of specimens was collected. In November and December o, the same year, Dr. H. H. Allan and Mr. J. D. Barron added to our collections considerably from the same locality, as did Dr. Cockayne when he again visited the mountain in January 1929.

At the base of the mountain *G. oppositifolia* abounds and then, on ascending, it is noticed that the plants, though erect in habit, are bearing smaller and alternate leaves, while the inflorescences are becoming more axillary. It was among these plants that it was noticed the calyces were becoming fleshy and then a plant was found with some of the calyx segments dry, as in *G. oppositi- folia*, while some were fleshy like those of *G. antipoda*. On ascending the

mountain further the Gaultherias become more prostrate and have thicker leaves with undulate margins, while the flowers are borne either singly in the leaf-axils or on very few-flowered axillary racemes. These forms gradually pass over into typical *G. antipoda*. In the forms which approach more nearly to *G. oppositifolia*, the leaves are broader and longer than in those showing closer affinity to *G. antipoda*, and they are also distinctly cordate at the base—the *antipoda*-like specimens having more ovate leaves.

The Volcanic Plateau district at Whakarewarewa heath and the cliffs on the shores of Lake Rotorua, where both Cockayne and Allan have collected specimens, is another good locality for these hybrids. Cockayne collecting in December 1905 remarks on the great hybrid swarm on the heath where *G. oppositifolia* predominates. These hybrids are comparable in all their gradations with those growing on Rainbow Mountain.

In the East Cape district again a similar state of affairs exists and Allan, collecting on a small hill between Tarawera P.O. and the foot of Turangakama Hill in November 1928, has sent to Kew a set of characterisitc hybrids between the two species.

Dr. Cockayne has sent an interesting specimen collected by T. Kirk near Lake Tarawera, probably long before the eruption of Mt. Tarawera. This is labelled *G. oppositifolia* by Kirk, but from its hairy stems and alternate leaves it is obviously a hybrid with *G. antipoda*, though its mainly terminal inflorescences show its close affinity to *G. oppositifolia*.

The hybrid Gaultherias, like so many of the other New Zealand hybrids, set fertile seed, and a number of seedlings have been raised at Kew from the seed found on the specimens collected in New Zealand. It is interesting to notice that among the few seedlings raised at Kew some were fairly uniform and usually resembled the parent plant, while in others the progeny was mixed and some of the seedlings were nearer to *G. antipoda*, while others resembled *G. oppositifolia* in habit and leaf shape. It is hoped that a careful study of seedlings from seeds of natural hybrids may be made in New Zealand and the character of the progeny noted, since much of interest might be learnt by recording the types of offspring from known parents of these fertile hybrids.

Gaultheria paniculata × G. oppositifolia

NEW ZEALAND. North Island :

Volcanic Plateau District :—Rainbow Mountain, Dec. 1928, *Barron*.

This is the only specimen we have seen which points to the existence of hybrids between *G. paniculata* and *G. oppositifolia*. These two species differ in little but the shape of the leaves. In Barron's specimen they are broadly triangular-lanceolate and rounded at the base, 4 cm. long and 1·5 cm. broad at the broadest part, and are intermediate between those of the parents. The presence of a few strigose hairs on the young branches and leaves and the indumentum of the pedicels, which is a minute pubescence with occasionally one of the thicker hairs found in *G. paniculata*, also point to this plant being a hybrid.

Gaultheria paniculata × G. antipoda

? *Gaultheria divergens* Colenso in Trans. N.Z. Inst. xx, 198 (1897).

NEW ZEALAND. North Island :

Volcanic Plateau District :—Rainbow Mountain, Dec. 1928, *Barron*. Rotorua road, Taupo, Nov. 1897, *Petrie* (4207 in Herb. Cockayne). Mount Tongariro, west side, County of East Taupo, 1887, *H. Hill* (type of *G. divergens* Colenso). Waimarino, *Cockayne* 4216. Sulphur Stream, west flanks of Ruapehu, Jan.–Feb. 1929, *Mrs. Martin* (4301, 4302 in Herb. Cockayne). Mangaone, Raetihi, near Ruapehu, 1933, *Attwood*, K. 1, 2, 3, 4, 5, 6, 8, 9, 18, 19, 20, 25, 27, 28, 29, 38, 39, 40. Headwaters of Wanganui River, draining from Mount Ruapehu, July 1933, *Attwood*, K. 43, 44, 48, 49, 51.

Egmont–Wanganui District :—Mount Egmont, *Dieffenbach*.

Nothing resembling Dieffenbach's specimen has been collected on Mount Egmont since his visit, and it will be remembered that careful search by Cheeseman and others on the mountain failed to reveal *G. oppositifolia*, although there is a specimen at Kew collected by Bidwill and labelled from Mount Egmont.

The type specimen of *G. divergens* Colenso differs from the other specimens enumerated in having much thicker leaves. This suggests that *G. Colensoi* may be concerned in the cross, but information is insufficient to settle the point.

PERNETTYA.

After careful consideration of the genera *Gaultheria* and *Pernettya*, we have decided to describe four species of *Pernettya*, two from New Zealand, *P. nana* Colenso and *P. macrostigma* Colenso (*Gaultheria perplexa* T. Kirk), and two from Tasmania, *P. tasmanica* Hook. fil. and *P. lanceolata* (*Gaultheria lanceolata* Hook. fil.).

We consider Colenso was correct in placing his plant, which he found at Glenross Station, Hawke's Bay County, in the genus *Pernettya*, and we are therefore restoring his name *P. macrostigma* which he gave to this specimen, and which later was named *Gaultheria perplexa* by Kirk.

Similarly, Hooker's *Gaultheria lanceolata* from Tasmania, from its fruit characters, is an exact counterpart of ' *G. perplexa* ' and should, we consider, be regarded as a *Pernettya* rather than a *Gaultheria*. The calyx character in these two genera is by no means a good distinguishing character. For in some Gaultherias, such as *G. oppositifolia* and *G. rupestris*, the calyx segments never become fleshy when the fruit ripens, while some forms of *G. antipoda* have a dry calyx and others have the characteristic fleshy one ; then again in some of the South American Pernettyas, especially *P. Pentlandii* (Bot. Mag. 6204), the calyx segments of the ripe fruit are fleshy, while they are partly so in *P. pumila* of the Falkland Islands. The only satisfactory distinguishing character between the two genera is in the fruit, *Pernettya* having a fleshy berry and *Gaultheria* a dry dehiscent capsule.

A somewhat similar difficulty with regard to these two genera occurs with the Falkland Islands and Patagonian species. Skottsberg (15) figures the calyx segments of *Pernettya pumila* slightly swollen in the ripe fruit, while in *Gaultheria antarctica* Hook. fil. (*G. microphylla* (Forst. fil.) Hook. fil., pro parte), he figures swollen calyces varying from the condition found in *G. depressa* to that found in *Pernettya macrostigma* or *P. lanceolata*. In the latter condition, when the calyx does not embrace the fleshy fruit, he says ' the fruit is then no capsule, but a berry as in *Pernettya* (pl. ii, fig. 10) '. He finds intermediate forms most common, the lower half of the fruit wall being thin and surrounded by the calyx lobes and the upper half more fleshy. ' It seems ', he adds, ' as if the limits between the two genera are very vague indeed ', and he points to *P. pumila* where the lower part of the calyx always becomes slightly enlarged as the fruit matures. A good type of the intermediate state is shown by the specimen collected by Skottsberg at Navy Point, Stanley Harbour, where the fruit is a berry with the much swollen calyx below it (pl. ii, figs. 5, 9, & 10), exactly like the fruits of *Pernettya macrostigma*, and Skottsberg (17) in his later paper on the vegetation of the Andes, when discussing *G. serpyllifolia* (*G. antarctica*) mentions that he considers it not improbable that the intermediate Falkland Island specimens are hybrids between *G. serpyllifolia* (= *G. antarctica*) and *Pernettya pumila*.

Skottsberg is probably correct in suggesting these Falkland Islands' specimens are bi-generic hybrids, and it seemed possible that a similar explanation might be required to account for the Tasmanian *Pernettya lanceolata* and for *P. macrostigma* from New Zealand. In both these, however, the specimens from different collections and different localities appear too uniform to warrant such a possibility, and it seems far more reasonable to regard them as definite species bridging these two genera, which, in the Southern Hemisphere especially, cannot be very definitely separated ; moreover, *P. tasmanica*, which is an undoubted *Pernettya*, also has a fleshy calyx and thus adds to the difficulty of an exact separation of these two genera. Although *Pernettya tasmanica* and *G. hispida*, which might be the parents of *P. lanceolata*, have been collected growing together at Dry's Bluff in the Tasmanian Mountains by A. V. Giblin, the uniformity of *P. lanceolata* in all its characters seems fully to support the accepted view that it is a true species. Again, the New Zealand *P. macrostigma* is also so uniform and is so widely distributed (North, South, and Stewart Islands) that the rare and restricted *P. nana* could hardly be one of its parents. We have, therefore, very little hesitation in maintaining it as a distinct species.

P. macrostigma, however, hybridises freely with *Gaultheria depressa*, when they are growing together, and a good series of hybrid forms was found by the senior author at Waimarino, near the National Park Station (North Island), in 1928. A very similar form collected by Messrs. Simpson and Scott Thomson on Flagstaff Hill, Dunedin, should also be regarded as a hybrid between *G. depressa* and *P. macrostigma*. Both species grow together on the spot, and the specimens in question have dark red fruits and swollen calyces ;

Cockayne writes : ' had it not been constant, I would have said *G. depressa*×
G. perplexa '.

Though these specimens are fairly uniform, they possess the strigose stem-
hairs of *G. depressa*, and in both leaf- and fruit-characters they are inter-
mediate between the probable parents ; it seems highly likely, therefore,
it is a hybrid as suggested, despite the fact that this form ' covers acres '.
There are other specimens which may be attributable to this parentage and also
several which we consider are the result of the cross *P. macrostigma*×*G. rupestris*
(prob. var. *parvifolia*). In this we agree with Cockayne, who has definitely
labelled one specimen collected by Allan on Mt. Peel (South Island) as ' *G. per-
plexa*×*rupestris* ' ; there are several others which puzzled earlier botanists
which exactly match this specimen. Some of these were regarded by
Hooker (10) as possible varieties of *G. rupestris*, but we consider they are in
reality hybrids between *G. rupestris* and *P. macrostigma*.

The plant described by Colenso* as *Pernettya polyphylla* is actually *Penta-
chondra pumila* R. Br. (Epacridaceae).

Key to the New Zealand and Tasmanian species of Pernettya.

Erect plants with a woody stock and ascending branches, up to
    about 30 cm. high, leaves lanceolate, averaging about 1·7 cm.
    long and 0·5 cm. broad, flowers solitary or occasionally sub-
    racemose towards the end of the branches ; pedicels about
    6 mm. long, with about 6 scattered bracteoles ; flowers white ;
    anther cells biaristate ; fruiting calyx fleshy ; berry half
    exserted from the calyx, rather thin-walled ....   1. *P. lanceolata.*
Dwarf or trailing plants ; leaves generally less than 1 cm. long.
    Trailing plant with wiry branches, the young ones sparingly
      setose ; leaves usually linear, about 0·8–1 cm. long and
      0·4 cm. broad ; flowers solitary ; pedicels 2–3 mm. long with
      several small bracteoles ; calyx segments shortly but con-
      spicuously ciliate ; anther cells conspicuously biaristate ;
      fruiting calyx fleshy ; fruit baccate, half exserted from the
      fleshy calyx ....   2. *P. macrostigma.*
Dwarf compact plants with numerous small leaves.
    Filaments ribbon-like, gradually and evenly widened towards
      the base, smooth ; anther cells with two short rigid awns.
      Leaves up to 3–6 mm. long and 1–2 mm. broad ; flowers
      solitary ; pedicels about 3 mm. long with 3–4 bracteoles ;
      calyx segments ciliate, fruiting calyx fleshy ; fruit baccate
      (sometimes thin-walled ?) ....   3. *P. nana.*
    Filaments with a distinct swelling towards the base, papillose ;
      anther cells awnless. Leaves up to 8 mm. long and 3 mm.
      broad ; flowers solitary ; pedicels about 3 mm. long with
      about 4 bracteoles ; calyx segments ciliate ; fruiting calyx
      fleshy ; fruit baccate ....   4. *P. tasmanica.*

* Trans. N.Z. Inst. xxxi, 274 (1899).

1. **Pernettya lanceolata** (*Hook. fil.*) *B. L. Burtt et A. W. Hill*, comb. nov.

Gaultheria lanceolata Hook. fil. in Hook. Lond. Journ. Bot. vi, 267 (1847) ;
Fl. Tasman. i, 241 & t. 72* (1857) ; Bentham, Fl. Austral. iv, 141 (1869) ;
Rodway, Tasman. Fl. 108 (1903).

Brossaea lanceolata (Hook. fil.) O. Kuntze, Rev. Gen. 388 (1891).

TASMANIA. Ben Lomond, 1835, *Gunn* 515. Summit of Western Mountains,
May 1845, *Gunn* 515. Dry's Bluff, North Spur, 1050 m., April 1929, *Giblin
& Long* 2 (585 in Herb. Tasm. Mus.).

Hooker, in his original description of the fruit, writes : ' *Capsula* magna,
coriaceo-carnosa, ovata, truncata, irregulariter rupta ? *Pisi sativi* magnitudine,
basi calycis ampliati et incrassati sed non baccati immersa.' In the ' Flora
Tasmanica ', however, he definitely states ' calyce baccato ' and ' calyx baccate,
red '. Bentham, in the ' Flora Australiensis ', writes : ' Fruiting calyx berry-
like, red, more or less enclosing the fruit '.

In spite of Hooker's definite statement that the fruit is ' coriaceo-carnosa '
all authors have previously retained the species in *Gaultheria*. Recently,
however, further material of this species has been sent to Kew by Mr. A. V.
Giblin, and it is now clear that there is no structural difference between the
fruits of *P. lanceolata* and *P. tasmanica*, although the fruit of *P. lanceolata*
is slightly less fleshy than that of *P. tasmanica*. Similar, slightly fleshy, thin-
walled, indehiscent (? or irregularly rupturing) fruits are also found on some
specimens of *Pernettya* from Colombia.

The calyx in *P. lanceolata* becomes very swollen and fleshy in all parts as
the fruit ripens and the fleshy berry protrudes from the swollen cup-like calyx.
The fruit is described as red or rose-coloured. The anther cells are provided
with two distinct awns to each cell.

2. **Pernettya macrostigma** *Colenso* in Trans. N.Z. Inst. xxi, 92 (1888).

Gaultheria antipoda var. *microphylla* Hook. fil. Fl. N.Z. i, 161 (1854), partim ;
Handb. N.Z. Fl. i. 174 (1864), partim ; Cheeseman, Man. N.Z. Fl. [ed. 1], 406
(1906).

Gaultheria depressa var. *microphylla* (Hook. fil.) Cheeseman, Man. N.Z. Fl.
ed. 2, 690 (1925).

Gaultheria perplexa T. Kirk in Trans. N.Z. Inst. xxix, 538 (1897), nomen ;
Cheeseman, Man. N.Z. Fl. [ed. 1], 406 (1906) ; Illustr. N.Z. Fl. t. 122 (1914) ;
Man. N.Z. Fl. ed. 2, 609 (1925).

The illustration published by the New Zealand Education Department (14)
as *G. perplexa* actually depicts a plant of *G. rupestris*.

NEW ZEALAND. North Island : Open grounds on dry hills in the interior,
Glenross Station, County of Hawke's Bay, Dec. 1887, *Balfour* (type!). [Ap-
parently also at Waimarino (*A. W. Hill*), but all the specimens collected were
hybrids with *Gaultheria antipoda*.]

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* In this plate the anther cells are shown bearing only one awn instead of two, as is
actually the case.

NEW ZEALAND. South Island :

Sounds–Nelson District :—Kerr's Hill, Kikiwa, c. 600 m. : forming prostrate open mats with interlacing branches ; a linear-leaved jordanon also common in adjacent part of North-Western district: Jan. 1929, *Allan* 550 A. Buller Valley, Nelson, *Cheeseman.*

North-Western District :—Rotuiti Lake, *Monro* 146.

South Otago District :—Flagstaff Hill, Dunedin, c. 600 m., Nov. 1927, *Watt* ; Dec. 1928, *J. Scott Thomson & Simpson* (4229, 4230, 4231, 4232, 4233, 4296 in Herb. Cockayne). Bluff Harbour, on ancient dune, Nov. 1905, *Cockayne*

Fig. 5.—*Gaultheria depressa* ×
Pernettya macrostigma.

A. Fruiting shoot (nat. size).
B. Fruit and fleshy calyx in longi-
    tudinal section (× 3).
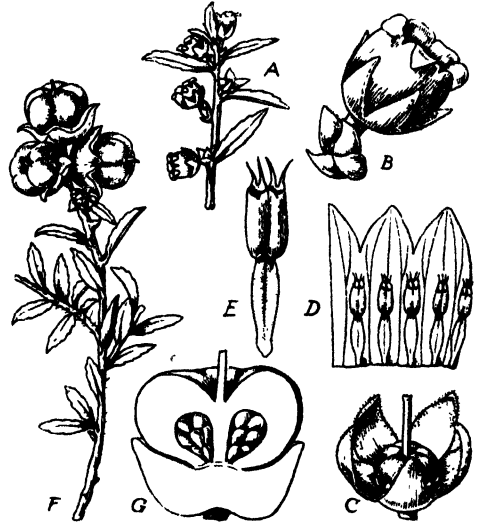
Fig. 6.—*Pernettya macrostigma* Colenso.

A. Flowering shoot (nat. size).
B. Flower (× 4).
C. Calyx and gynaecium (× 6).
D. Part of corolla and androecium (× 6).
E. Stamen (× 12).
F. Fruiting branch (nat. size).
G. Berry and fleshy calyx in longitudinal
    section (× 3).

4219. Bluff Island, fruit baccate and enlarged, *Lyall.* Bluff Hill, stems wiry, straggling and procumbent, leaves narrow-linear with distant serratures, flowers axillary, calyx persistent, fleshy, supporting the berry ; remarkably constant in its characters : Nov. 1883, *Kirk* 1028 (type of *G. perplexa* T. Kirk).

Stewart District :—Stewart Island, *Kirk* ; Stewart Island, Mason Bay, 1910, *Murdoch* (570, ex herb. Petrie).

P. macrostigma is a straggling prostrate shrub with wiry interlaced branches. The leaves are thick, linear acute, with serrate margins, and the flowers are

axillary. Its systematic position has long been a puzzle, and this is reflected in the specific name ' *perplexa* ' given by Kirk, by which name under the genus *Gaultheria* it has so long been known. Owing to the fruit being a berry it is necessary to restore it to the genus *Pernettya*, where it was placed by Colenso.

P. macrostigma hybridises freely with *Gaultheria*, and at Waimarino, where a series of the bigeneric hybrids was found, specimens of pure *P. macrostigma* were unfortunately not collected in the short time available. (Fig. 6.)

HYBRIDS :—

    × *G. antipoda* Forst. fil. (p. 641).

    × *G. depressa* Hook. fil. (p. 642).

    × *G. rupestris* var. *parvifolia* Hook. fil. (p. 642).

    × *G. Colensoi* Hook. fil. (p. 643).
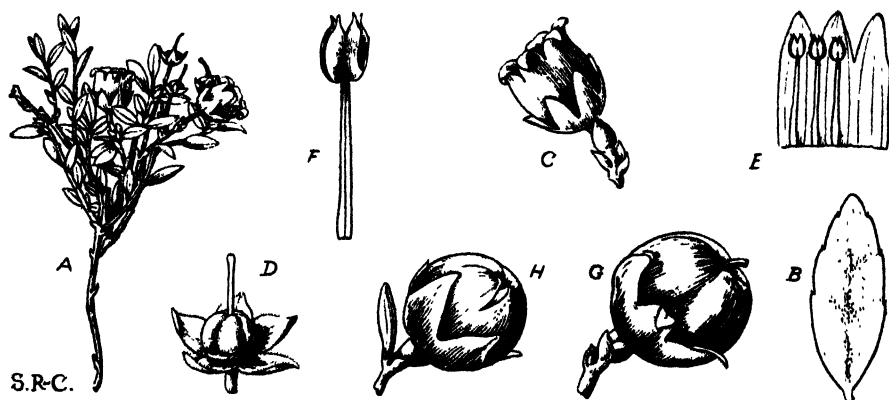
FIG. 7.—*Pernettya nana* Colenso.

A. Flowering shoot (nat. size).   B. Leaf (× 6).   C. Flower (× 4).   D. Calyx and gynaecium (× 4).   E. Part of corolla and androecium (× 4).   F. Stamen (× 8).   G. Berry and persistent calyx (× 3).   H. Less fleshy berry and persistent calyx (× 3).

3. Pernettya nana Colenso in Trans. N.Z. Inst. xxiii, 389 (1891) ; Cheeseman, Man. N.Z. Fl. [ed. 1], 408 (1906) ; ed. 2, 692 (1925).

Pernettya tasmanica Hook. fil. Handb. Fl. N.Z. i, 176 (1864), non Lond. Journ. Bot. vi, 268 (1847).

Pernettya tasmanica var. *neo-zelandica* T. Kirk in Trans. N.Z. Inst. xxvii, 351 (1895).

NEW ZEALAND.   South Island :

Eastern District.   Mountains above Broken River, 1880, *Kirk* 927.   Top of Lake Pukaki, on dry grassy slopes, *Petrie* (11,075 in Herb. Pl. Res. Stat.). River Thomas flat, Waimakariri River basin, 600 m., Nov. 1898, *Cockayne* 6203.

THE GENERA GAULTHERIA AND PERNETTYA

Western District. Tasman Valley, Mount Cook, Feb. 1911, *Petrie* (11,074 in Herb. Pl. Res. Stat.).

Pernettya nana forms a close low mat and is nearly allied to *P. tasmanica*, but is a smaller plant in every way, especially in its leaves. Like *P. tasmanica* the calyx continues to grow as the fruit ripens and becomes fleshy at the base, forming a cup from which the fleshy berry protrudes ; the free portions of the calyx segments, however, remain herbaceous. In some specimens the berry appears to be of the thin-walled type found in *P. lanceolata* (fig. 8, H). The smooth ribbon-like anther filaments of this species are very distinct from those of any other *Pernettya*. (Fig. 7.)

HYBRID :—

> ✕ *Gaultheria rupestris* var. *parvifolia* Hook. fil. (p. 644).

4. **Pernettya tasmanica** *Hook. fil.* in Hook. Lond. Journ. Bot. vi, 268 (1847) ; Fl. Tasm. i, 242, t. 73 (1860) ; Bentham, Fl. Austr. iv, 140 (1869) ; Rodway, Tasm. Fl. 108 (1906) ; Gard. Chron. ser. 3, xciv, 325 (1933).

TASMANIA. Port Arthur, *Backhouse*. Western Mountains, Feb. 1843, *Gunn*, 708/1842. Hampshire Hills, Feb. 1837, *Gunn* 708/1837. Lake St. Clair, Feb. 1845, *Gunn* 708. Summit of Western Mountains, May 1845, *Gunn* 708. Arthur's Lakes, Jan. 1845, *Gunn* 708. Mt. Field East, 1078 m., Jan. 1915, *Gibbs* 6798. Lake Fenton, Mt. Field, 1170 m., Dec. 1929, *Lord* (Herb. Tasm. Mus. 583). Dry's Bluff, 1078 m., March 1929, *Giblin & Long* (Herb. Tasm. Mus. 583).

When describing this species Hooker created a new subgenus, *Perandra*, for it, since he could not find awns on the anther cells. This character, however, is not constant, as anthers with minute points have been found on some of the specimens. In the closely allied *P. nana* there are distinct, short, rigid awns on the anther cells which much resemble those found in the South American *P. pumila*, the type species of the genus. *P. furens* (Hook. & Arn.) Klotzsch— which has also been referred to this subgenus—is not closely related either to *P. nana* or *P. tasmanica*, being a shrub with large leaves and racemes of flowers. The subgenus therefore is not being maintained.

The fruit of *P. tasmanica* is a red berry and resembles that of *P. nana* in having the calyx somewhat enlarged and fleshy at the base when the fruit is ripe. As in *P. nana* the calyx enlarges as the fruit ripens and the basal portion becomes fleshy, while the free portions of the segments remain green and herbaceous.

<p align="center">GAUTHERIA ✕ PERNETTYA HYBRIDS.</p>

Gaultheria antipoda ✕ Pernettya macrostigma

NEW ZEALAND. North Island :

Volcanic Plateau District :—' Dry heights in the Taupo country, like 984 [*Gaultheria depressa* Hook. fil.], low and prostrate, but very distinct : fruit

small, red and not good eating ' *Colenso* 985. ' Top of Tiliokura—the high ridge west of Hawkes Bay and bounding same : small plant, 6 inches high,' *Colenso* 2401. Tongariro-Ruapehu, near River Waihohun, c. 1110 m.; ' creeping underground on gravelly banks (pumice) and forming mats ', 26 Jan. 1908, *Cockayne* 4218. West slope, Mount Ruapehu, banks of Sulphur stream, c. 900 m., Jan.–Feb. 1929, *Mrs. Martin* (4300 in herb. Cockayne).

NEW ZEALAND.   South Island :

Sounds–Nelson District :—Kerr's Hill, Kikiwa, 600 m., 'An erect, densely branched, semi-divaricating shrub ', 27 Jan. 1929, *Allan* 550 c.

South Otago District :—Hills round Dunedin, 300 m., low wiry shrub, 1864– 1865, *Hector & Buchanan* 125, 126. Signal Hill, Dunedin, 210 m., 23 Dec. 1910, *Petrie* 563. Flagstaff Hill, Dunedin, shrub 60 cm. high, calyx not swollen, Dec. 1928, *J. Scott Thomson & Simpson* (4227 in herb. Cockayne).

Western District :—Landsborough River, March 1927, *Dalrymple* 572.

The hybrids are more erect in growth than those between *G. depressa* and *P. macrostigma* and also have larger leaves. The fruits as a rule have the calyces very little swollen, sometimes hardly at all. When swollen it appears that this takes place only at the base of the calyx.

Gaultheria rupestris var. parvifolia × Pernettya macrostigma

NEW ZEALAND.   South Island :

Sounds–Nelson District :—Upper Wairau, 1850, *Monro* 90.

Eastern District :—Mount Rawley, 660 m., May 1860, *Sinclair & Haast* 250. Mount Peel, c. 600 m., Dec. 1919, *Allan* 574.

Only isolated specimens of this hybrid have been collected. The leaves of the intermediate specimens average about 1·5 cm. long and 3–4 mm. broad, and are of the thick texture associated with *G. rupestris* var. *parvifolia*. The flowers are usually in short racemes, but some may be solitary on the same plant. In some specimens the calyx has apparently continued to grow after the corolla has withered, but has not become fleshy : most of the fruits are dry capsules, but in a few specimens they are somewhat fleshy, indicating the *Pernettya* influence.

It is often difficult to distinguish between this hybrid and *Gaultheria antipoda* × *Pernettya macrostigma*.

Gaultheria depressa × Pernettya macrostigma

NEW ZEALAND.   North Island :

Volcanic Plateau District :—Near National Park Station, Waimarino, c. 900 m., ' prostrate on open boggy moorland ', Feb. 1928, *A. W. Hill* 2, 2 A.

NEW ZEALAND.   South Island :

South Otago District :—Flagstaff Hill, near Dunedin, ' Swollen calyces. Fruits always dark red. Capsules equalling calyces. This is a good jordanon.

No question about it ; covers acres ', March 1929, *J. Scott Thomson & Simpson* (4297 in herb. Cockayne).

At Waimarino, true *P. macrostigma* was unfortunately not collected, but the collections were made by the senior author near the station while waiting for the train and he was more interested in noticing the diversity of the hybrid forms. Further search would no doubt reveal the presence of *P. macrostigma* in the locality. With regard to the fruits it is of interest to notice that the swollen calyx is cup-like and encloses the fruit, thus being more like the fruit of *G. depressa* than that of *P. macrostigma*. This character is well seen in the Dunedin specimens. (Fig. 5.)

FIG. 8.—*Gaultheria rupestris* var. *parvifolia* × *Pernettya nana*.

A. Flowering shoot (nat. size). B. Leaf (×3). C. Flower (×4). D. Calyx and gynaecium (×6). E. Corolla, spread open, and androecium (×4). F. Abortive stamen (×16).

Gaultheria Colensoi × Pernettya macrostigma

NEW ZEALAND. North Island :

Volcanic Plateau District :—Taupo, June 1850, ' small, rambling, low shrub, plains ', *Colenso* 2379.

The determination of this specimen, which bears the MS. name *G. neglecta* W. C. on the Kew sheet, is proposed with some reserve. Nevertheless, the linear or linear-lanceolate leaves and the ciliate calyx lobes are characters which it is suggested have been derived from *Pernettya macrostigma*, while the pubescent, but almost bristleless, branchlets, the texture of the leaves, rather

thicker than is usual in *Pernettya*, and the tendency for the flowers to form a terminal raceme all distinctly recall *Gaultheria Colensoi*.

This is one of those cases where artificial crossing of the two plants by botanists in New Zealand is needed to settle the question definitely.

Gaultheria rupestris var. parvifolia × Pernettya nana

NEW ZEALAND. South Island :

Fiord District :—Mount Earnslaw, Dec. 1927, *Allan* xxvi, 141.

This specimen is the only example of this hybrid known to us. *Pernettya nana* was recorded from Mount Earnslaw by Cheeseman, and *Gaultheria rupestris* var. *parvifolia* is common on the mountains of the South Island. As the figures show, it clearly combines the characters of the two parents. This is especially noticeable in the shape of the filaments, which are sterile, and the calyx lobes, with close short cilia as in *Pernettya nana* ; the leaves and inflorescences are also more or less intermediate in character. (Fig. 8.)

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NEW ZEALAND

N. AUCKLAND

S. AUCKLAND

VOLCANIC PLATEAU

EAST CAPE

EGMONT-WANGANUI

RUAHINE-COOK

SOUNDS-NELSON

N. WESTERN

N. EASTERN

WESTERN

EASTERN

MILFORD

N. OTAGO

S. OTAGO

STEWART

BOTANICAL DISTRICTS
AND RANGE OF —
1. G. oppositifolia
2. G. Colensoi
3. G. rupestris
     var subcorymbosa

[*Note.*—The botanical districts are indicated by dotted lines;
the range of the three species by dash and dot lines.]

An *Anemone* from New Zealand : a plant hitherto regarded as a species of *Ranunculus*. By J. PARKIN, M.A., F.L.S., and W. A. SLEDGE, Ph.D., B.Sc. (Department of Botany, University of Leeds).

(With 7 text-figures)

[Read 7 December 1933]

INTRODUCTION

In recent letters to ' Nature ' (5) we showed that the New Zealand plant first described by Cheeseman in 1885 and named by him *Ranunculus tenuicaulis* could not be a species of *Ranunculus* on account of its having a simple mono-seriate perianth, a suspended and not a basal ovule, and an involucre. We considered it, therefore, to be most likely a species of *Anemone*, a genus hitherto unrecorded for New Zealand.

Since then, thanks to abundant material, both dried and spirit preserved, kindly collected and sent to us by Mr. J. Scott Thomson of Dunedin, we have been able to examine the plant thoroughly, and find it to be not only a species of *Anemone*, but also, as might be expected, one peculiar to the Dominion.

Cheeseman probably never saw the plant in flower, having before him only fruiting specimens. In his original description he writes :—' Petals not seen.' Kirk (4) fourteen years later states :—' sepals not seen, petals 5, linear, acute.' In the interval he had evidently seen the plant in flower and, taking for granted the correctness of Cheeseman's diagnosis, misinterpreted the perianth, perhaps imagining the sepals to have fallen. In some species of *Ranunculus* the sepals are inclined to be caducous.

Cheeseman in his ' Manual of the New Zealand Flora ' (1906) describes the petals in the same terms as Kirk, not mentioning the sepals : and he repeats this description in the second edition (1925), the inference being that he had gleaned this information from Kirk's volume. There is no reference to the nectary—an invariable accompaniment of the *Ranunculus* petal. This is significant, since as a rule in describing the species of *Ranunculus* he lays stress on the character of the nectary.

Not having adequate material before him when he first described this plant, Cheeseman perhaps rather jumped to the conclusion that it must be a species of *Ranunculus*, a genus so well represented in New Zealand ; while *Anemone* was unknown as a component of its flora. He remarks, however, on its peculiar achenes, which he says distinguish it from all other species of *Ranunculus* belonging to New Zealand.

Fig. 1. *Anemone tenuicaulis* (Cheesem.) Parkin & Sledge, slightly reduced. Fig. 2. Scape showing secondary flower bud, nat. size. Figs. 3 & 4. Sepals showing variation in form, ×3. Fig. 5. Stamen, ×3. Fig. 6. Carpel from open flower, ×3. Fig. 7. Ripe achene, ×3.

DESCRIPTION

ANEMONE TENUICAULIS (Cheesem.) Parkin & Sledge, comb. nov.

Ranunculus tenuicaulis Cheesem. in Trans. N.Z. Inst. xvii, 235 (1885) ; T. Kirk, Students' Fl. N.Z. xiv, 1899 ; Cheesem. Man. N.Z. Fl. 14 (1906) ; ed. 2, 442 (1925).

The rootstock is usually more or less vertical, but is inclined and branched in some specimens, the plant evidently propagating itself vegetatively to some extent. The length of the petioles and size of the leaves varies considerably ; in mature plants the petioles are usually more or less elongated, but sometimes they scarcely exceed 3 cm. in length. They are dilated below into membranous sheaths. Cheeseman describes the leaves as ' cut to the base into 3, rarely 5, broadly cuneate divisions ', but in all the specimens we have examined they are tripartite, the lateral segments being sometimes so deeply lobed as to give the leaf a 5-partite appearance. The middle segment is usually somewhat symmetrically trilobed, the lobes being either entire or often the central and sometimes the lateral ones bearing two to three acute or subacute teeth. The lateral segments are regularly or irregularly bi- to tri-lobed, often deeply so, and frequently again toothed. A few shining hairs are always present on the upper surface of the leaf in the Swampy Hill plants, and the margins of the leaflets are constantly more or less ciliate. The under surface is glabrous.

One or two (rarely three) simple unbranched scapes are produced with an involucre of three foliaceous bracts variously placed according to development, at first close under the flower bud, but finally situated about the middle of the scape in the fruiting stage. The involucral leaves are usually unequal, rarely all simple, linear, entire, and acute, more often one or two and sometimes all three leaves being more or less deeply bi- or tri-lobed. Occasionally a second flower is produced from the involucre (fig. 2), but its peduncle does not elongate and it remains more or less hidden ; nor have we seen an open second flower, though its sepals, stamens, and carpels are fully formed. Both the dull red colour and the shape of the flowers are very characteristic. The widely spreading sepals (five to six, rarely seven) taper evenly to an acute apex from the suddenly rounded base, and adjacent sepals overlap at the base only, giving the flower a star-like appearance. The number of stamens ranges from six to fourteen, and averages nine in the thirty-four flowers examined. The number of stamens is always exceeded by the number of carpels. The filaments are thread-like, and the connective produced slightly beyond the pollen sacs. The carpels vary from fourteen to thirty-four, the average for fifty flowers being twenty-one. Cheeseman (2) gives the achenes as varying from five to twenty and being ' loosely packed ', but this statement was presumably based on over-ripe specimens from some of which achenes had already become detached. The achene excluding the style is 4–5 mm. long. The style is bent at its apex in the form of a hook, the tip of the hook

being somewhat spirally twisted (fig. 7). Cheeseman especially remarks on this achene as being peculiar for *Ranunculus*, and describes its style as spirally recurved. As the achene ripens the style hardens and darkens in colour and becomes an organ for the distribution of the seed. In the ripe seed the embryo, though quite small, has its two cotyledons clearly differentiated.

Distribution. Cheeseman (2) cites two localities in the Tararua Mountains in the North Island, and, in the South Island, single localities in Nelson and Canterbury, and many stations in Otago, which is evidently the headquarters of the species.

Habitat : Damp shady hill-sides. We are indebted to Mr. J. Scott Thomson for a list of plants associated with *Anemone tenuicaulis* at Swampy Hill near Dunedin. These include *Hebe buxifolia, Coprosma parviflora, Gaultheria perplexa, Cassinia fulvida, Ranunculus rivularis, R. lappaceus* var. *multiscapus, Carex ternaria, Danthonia Raoulii* var. *flavescens,* and *Hierochloe redolens.*

<p align="center">AFFINITIES</p>

Since the classification of the genus by Prantl (1887) and reproduced in ' Die Naturlichen Pflanzenfamilien ' in 1891, two important papers bearing on the taxonomy of *Anemone* have appeared. Janczewski (1892) in a morphological study of the genus shows that a group of species can be detached from Prantl's wide section, Anemonanthea, to form a separate one which he calls Rivularidium, deriving the term from the specific name of the best-known species belonging to this circle of affinity, viz., *Anemone rivularis.* Ulbrich, the chief living authority on *Anemone,* in his lengthy and exhaustive treatise (1906) on the taxonomy and geographical distribution of the genus, adopts Janczewski's innovation and rearranges the genus accordingly. In our consideration of the affinities of the New Zealand species we purpose following Ulbrich's classification.

The New Zealand species of *Anemone* undoubtedly belongs to the section Rivularidium, a position which might be expected from the standpoint of geographical distribution, and which in correspondence Dr. Ulbrich at once suggested for it.

As Ulbrich convincingly shows it is to the gynoecium rather than to any other part of the plant we must look for characters upon which to base primarily a natural classification of the genus ; and such characters are largely concerned with seed-dispersing mechanisms.

In the section Anemonanthea, as restricted by Ulbrich, the achene possesses no specialized contrivance for seed distribution. It is too heavy to be borne by the wind and too smooth to attach itself readily to animals, and further its style even if curved at the flowering stage does not harden at maturity into an organ particularly adapted for clinging to fur or feather. To this section belongs the common *Anemone* of the British Isles (*A. nemorosa*), and also such well-known ones in cultivation as *Anemone appennina* and *A. ranunculoides,*

In the section Rivularidium, on the other hand, as the comparatively heavy achene matures, the style hardens into a hook-like organ capable of attaching itself to animals. Further, the geographical distribution of the members of this section differs markedly from that of the foregoing in that there are no representatives in Europe or Africa. The species also extend further south. Indeed, they are found largely, though by no means exclusively, in the southern hemisphere, with the greatest development in South America.

Besides the above marks distinguishing these two sections Janczewski's researches (3) bring out others respecting the embryo. In species belonging to Anemonanthea the embryo of the ripe seed is an undifferentiated roundish mass of cells with no indication of the cotyledons. On the other hand, in Rivularidium the embryo is distinctly bifid, showing the rudiments of the two cotyledons. Correlated with this distinction is a difference in the dormant period of the seed. In Anemonanthea germination is deferred until the second spring following the maturity of the seed ; while in Rivularidium with the more differentiated embryo the seed germinates the spring following the ripening of the seed.

The ripe achene of *Anemone tenuicaulis* has not only the hooked and hardened style characteristic of the Rivularidium section, but also the bifid embryo. None of the fruits collected and sent to us by Mr. J. Scott Thomson in November 1932 has germinated. They were sown soon after their arrival in the early spring of 1933, but all rotted in the soil. We are consequently not yet in a position to pronounce definitely on the germination of the seed of *Anemone tenuicaulis*. To settle the matter it will be necessary to know how soon the seed germinates in New Zealand when sown immediately it is ripe.

Ulbrich enumerates thirteen species in all as belonging to the section of Rivularidium, and in the interval to date no further additions have been made except the one which forms the subject of this paper. The New Zealand species is not closely allied to any of these. In the form of its achene it comes nearest the Chilean species *Anemone antucensis*, but differs in having a single flowered scape, a less foliaceous involucre, and a thread-like instead of a flattened filament. It is probably more akin to the only other known Australasian species, *Anemone crassifolia*, of Tasmania, in spite of the striking difference in the outward appearance of the two plants, the Tasmanian species having a creeping rhizome, fleshy leaves, a much reduced involucre, and conspicuous white flowers. The star-like appearance of the New Zealand flower, unlike that of any other member of the Rivularidium section, is a distinctive feature. Considering the general lack of colour in New Zealand flowers, it is not a little remarkable that its *Anemone* should be red.

GEOGRAPHICAL DISTRIBUTION

The New Zealand fauna and flora, ever since their peculiar features were first recognised, have presented one of the most puzzling sets of problems in geographical distribution. This discovery of a single endemic species of an

interesting genus stimulates one to recall the speculations already made and
conclusions reached regarding the origin of this flora, with the hope thereby
of arriving at some plausible explanation as to how *Anemone* came to these
islands.

A notable component of the New Zealand flora is that part which is usually
spoken of as the northern or arctic, and the genus *Anemone* comes into this
category.   The general southward migration of northern forms is considered
to have taken place along the mountain ranges, the intervening tropical belts
being traversed in this way.   In the western hemisphere the Andes together
with the mountains of Mexico and central America provide an almost continu-
ous elevated track south.   In the eastern hemisphere, though the mountain
ranges are more detached, yet the evidence points to some migration of northern
forms south in this way.   Which path then it may be asked did *Anemone*
take to reach New Zealand ?

Ulbrich discusses in great detail the geographical distribution of *Anemone*.
On account of the number of endemics and also of species with discontinuous
distribution he considers the genus an old one geographically, though on these
grounds not all the sections appear to be of an equal age.   Among the older
sections he classes Anemonanthea and Rivularidium.   He considers that they
had a common origin at least as far back as the Oligocene in polar moors situated
in a region north of the Behring Straits.   On this supposition Rivularidium
moved southward in a westerly direction into Asia and in an easterly direction
into America, missing Europe.   Anemonanthea, on the other hand, spread
into Europe as well.   Both on account of its high endemism (twelve out of
fourteen species are to be regarded as endemic) and also its vegetative features
Rivularidium may be regarded as the older section, that is to say it has departed
less from the ancestral stock.   With the exception of *Anemone Richardsonii*
and *A. crassifolia*, which have developed creeping stems, the section Rivulari-
dium is without specialised means of vegetative increase.   On the other hand,
the species of Anemonanthea as a whole have creeping rhizomes or stolons.
In contrast to this, Rivularidium has developed a device for seed distribution,
while Anemonanthea has not.   These differences may in some measure account
for the distribution of the two sections at the present day.   Anemonanthea
has spread widely by land over the north temperate zone with few extensions
into the arctic.   Rivularidium, on the other hand, probably by means of its
achenes capable of attaching themselves to feathers, has been able to cross
seas and produce new species so far south as Tasmania and New Zealand.

Ulbrich is puzzled to account for the presence of a representative (*A. crassi-
folia*) of the section in Tasmania.   Any land connection between Australia and
Asia as a means is ruled out, since the former was already separated from the
latter before Tertiary times.   Hence he vaguely falls back upon birds as the
means of the transport from the Asiatic Continent.   Perhaps had he been
cognisant of the existence of *Anemone* in New Zealand he might have reasoned
differently.   It seems to us that *Anemone* more likely reached both Tasmania

and New Zealand by way of the Andes than from Asia. Even granted that these two species of the Antipodes came directly from stock nearly related to *Anemone rivularis*, an Asiatic origin for them need not follow, as this type is also represented in America. A direct transference by birds over the wide stretch of ocean which exists at the present day between South America and New Zealand is not to be inferred. In Tertiary times there is reason for believing that the Antarctic was much milder and so capable of supporting a varied flora. The extremity of South America is no great distance from Antarctic land·; hence northern plants which had travelled down the Andes, especially those capable of being distributed by birds or wind, might easily reach this new land and there spread and develop fresh forms. From this south polar land it is not difficult to imagine their passage northwards again to New Zealand and Tasmania respectively and perhaps independently.

On the analogy of other members of the family Ranunculaceae in the Antipodes the Andine rather than the Asiatic route is favoured. The species of *Caltha* found in New Zealand and Australia belong to the same section (Psychrophila) of the genus as do the species of South America—a section distinct from that which occurs in Europe, Asia, and North America. Though *Clematis* does not afford clear evidence in this direction, as the New Zealand species belong to a section of the genus widely spread over the world, yet they do show South American leanings. The single species of *Myosurus* occurring in New Zealand is closely allied to the South American one. Of the very few species of *Ranunculus* not endemic to New Zealand two are found also in the temperate South American region.

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